HARVEST INDEX VARIABILITY WITHIN AND BETWEEN FIELD PEA (*Pisum sativum* L.) CROPS.

A thesis
submitted in fulfilment of the requirements for the degree of

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Lincoln University
Canterbury
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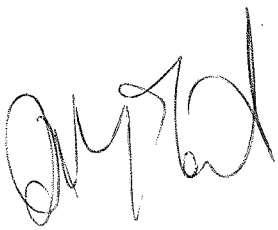
by

Derrick Jan Moot

1993

This is to certify that, with the following exceptions, the work described in this thesis was planned, implemented and described by Derrick Jan Moot under our direct supervision at Lincoln University.

- The selections of the genotypes, described in Chapter 3 were by Doctors P.D. Jamieson, W.A. Jermyn and, D.R. Wilson.
- The seed weight and plant weight measurements from the crops described in Chapter 3 were made by Teresa Windle.



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ABSTRACT

Abstract of a thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy at Lincoln University, New Zealand.

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The association between individual plant performance and seed yield variability within and between field pea crops was investigated. In 1988/89 six F8 genotypes with morphologically distinct characteristics were selected from a yield evaluation trial. Analysis of the individual plant performance within these crops indicated an association between low seed yields and the location and dispersion of plant harvest index (PHI) and plant weight (PWT) distributions. The analyses also showed there was a strong linear relationship between the seed weight (SWT) and PWT of the individual plants within each crop, and that the smallest plants tended to have the lowest PHI values.

A series of 20 simulations was used to formalize the relationships between SWT, PWT and PHI values within a crop into a principal axis model (PAM). The PAM was based on a principal axis which represented the linear relationship between SWT and PWT, and an ellipse which represented the scatter of data points around this line.

When the principal axis passed through the origin, the PHI of a plant was independent of its PWT and the mean PHI was equal to the gradient of the axis. However, when the principal axis had a negative intercept then the PHI was dependent on PWT and a MPW was calculated.

In 1989/90 four genotypes were sown at five plant populations, ranging from 9 to 400 plants m^{-2}. Significant seed and biological yield differences were detected among genotypes at 225 and 400 plants m^{-2}. The plasticity of yield components was highlighted, with significant genotype by environment interactions detected for each yield component. No relationship was found between results for yield components from spaced plants and those found at higher plant populations.

The two highest yielding genotypes (CLU and SLU) showed either greater stability or higher genotypic means for PHI than genotypes CVN and SVU. Despite significant skewness and kurtosis in the SWT, PWT, and PHI distributions from the crops in this experiment, the assumptions of the PAM held. The lower seed yield and increased variability in PHI values for genotype CVN were explained by its higher MPW and the positioning of the ellipse closer to the PWT axis intercept than in other genotypes. For genotype SVU, the lower seed yield and mean PHI values were explained by a lower slope for the principal axis.

Both low yielding genotypes were originally classified as having vigorous seedling growth and this characteristic may be detrimental to crop yields. A method for selection of field pea genotypes based on the PAM is proposed. This method enables the identification of weak competitors as single plants, which may have an advantage over vigorous plants when grown in a crop situation.

KEY WORDS: *Field peas, conventional leafed, semi-leafless, harvest index variability, principal axis model, yield components, minimum plant weight, ideotype, seedling vigour.*

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
CHI	Crop harvest index
CLN	Conventional low vigour non-uniform
CLU	Conventional low vigour uniform
CV	Coefficient of variation
CVN	Conventional vigorous non-uniform
CVU	Conventional vigorous uniform
DAS	Days after sowing
FD	Frequency distribution
GXE	Genotype by environment interaction
GHI	Genetic harvest index
LA	Lower apex
MBW	Minimum branch weight
PAM	Principal axis model
PAR	Photosynthetically active radiation
PHI	Plant harvest index

PWT	Total above ground dry weight for an individual plant
$\overline{PWT}$	Mean above ground dry weight from individual plants
R^2	Coefficient of determination
RGR	Relative growth rate
SD	Standard deviation
SEM	Standard error of the mean
SLU	Semi-leafless low vigour uniform
SVU	Semi-leafless vigorous uniform
SWT	Seed weight for an individual plant
$\overline{SWT}$	Mean seed weight for individual plants
UA	Upper apex
MPW	Minimum Plant Weight

CHAPTER ONE

GENERAL INTRODUCTION

1.1 BACKGROUND

Field pea (*Pisum sativum*) crops occupy about 20,000 ha in New Zealand, with most of this area in Canterbury (White, 1987). Peas are grown for cash returns and as a break crop for disease control and soil fertility improvement in mixed cropping rotations (White, 1991). They can produce high yields under favourable conditions. However, field pea crops exhibit poor stability of yield compared with other crops and so their average yield, over a range of growing conditions and seasons, is relatively low (Hedley and Ambrose, 1981; White, 1987; Wilson, 1987; Kelly, 1987). An important research goal is, therefore, to increase the average seed yield of field pea crops through improved understanding of the factors responsible for yield variability between genotypes, sites and seasons. Once these factors have been identified, their effects can be reduced through improved crop management techniques or selection strategies in breeding programmes.

The total seed yield per unit area of field pea crops has often been described by the numbers of plants per unit area, pods per plant, peas per pod and the mean seed weight (Falloon and White, 1978; Greenwood and McNamara, 1987) which are collectively defined as the yield components. Attempts to overcome low and variable yields have aimed at exploiting the differences in these yield components to produce higher yielding cultivars (Cousin, et al., 1985; Wilson, 1987). However, environmental variability in yield components between genotypes is high, with a large degree of interdependence, or

'plasticity' (Donald and Hamblin, 1976; Wilson, 1987), so their overall effectiveness as selection criteria is low (Samad, 1988).

As an alternative to the yield component approach for the description of crop yields, Ambrose and Hedley (1984) examined the variability within pea crops of seed weight per plant (SWT), above ground dry weight per plant (PWT) and the plant harvest index (PHI), defined as (SWT / PWT)*100 by Donald and Hamblin (1976). Ambrose and Hedley (1984) found that the distribution of PHI values within a population of plants was a strong determinant of variability in seed yield and crop harvest index (CHI); where CHI is (seed yield / biological yield)*100 (Donald and Hamblin, 1976), and the biological yield is the total above ground biological yield per unit area. Specifically, at a commercial population of 100 plants m^{-2}, Ambrose and Hedley (1984) observed that plants from genotypes with a high seed yield generally had a narrow range of PHI values (40-70 %), with less than 3 % of them barren (PHI=0 %). In contrast, one genotype with a low seed yield had a wide range of PHI values (0-70 %) with 27 % of its plants' barren. Individual plants with low PHI values also tended to have low PWT values (Hedley and Ambrose, 1985). These plants with a low PHI utilize resources and contribute to the biological yield of a crop but do not produce a significant proportion of its seed yield. Such plants therefore reduce the potential CHI and seed yield of a crop.

Despite variation in PHI values within crops, genotypic differences in the potential for partitioning dry matter to seed were small (Hedley and Ambrose, 1984). Similar maximum PHI values of between 65 and 70 % were measured for all of the genotypes they examined. Based on these results, Ambrose and Hedley (1984) hypothesized that improved seed yields would come from selecting genotypes that produce a uniform and high PHI value for all plants in the crop, rather than by selecting to increase their potential PHI. Furthermore, uniformity in PHI values may result from selection of

specific morphological characteristics. These characteristics could then be incorporated into a crop ideotype, to reduce interplant competition and consequently the proportion of small plants in the crop (Hedley and Ambrose, 1981).

A major practical problem is to define the plant types or morphological characters associated with consistent high PHI values for all plants in a community. Traditionally, plant types have been selected in early generations of pea breeding programmes for their superior performance as single plants. The plants chosen usually exhibit vigorous growth and are highly competitive. Ambrose and Hedley (1984) suggested these competitive plant types would result in a high degree of variation in PHI values from plant to plant and consequently produce low CHI values, when grown in crop communities. To achieve a stable high CHI and therefore seed yield, the ideal plant type may be non-competitive and semi-leafless, with poor performance as a single plant. This idea is similar to that proposed by Donald (1968) for crop ideotypes in general.

1.2 RESEARCH OBJECTIVES AND ASSUMPTIONS

The objective of the research reported in this thesis is to determine whether high variability in seed yields of field pea crops is associated with plant types that produce variable PWT and PHI distributions, as hypothesized by Ambrose and Hedley (1984).

Central to this objective are two assumptions that required further testing:

Assumption 1: Seed yield variability could be related to differences in PHI and PWT distributions, as proposed by Ambrose and Hedley (1984). While investigating this relationship it became evident that these associations needed to be formalized into a testable system from which selection criteria could be identified for use in a breeding programme.

Assumption 2: Environmental variability in yield components between the selected genotypes would be high, and consequently the effectiveness of yield components as selection criteria would be low (Wilson, 1987; Samad, 1988).

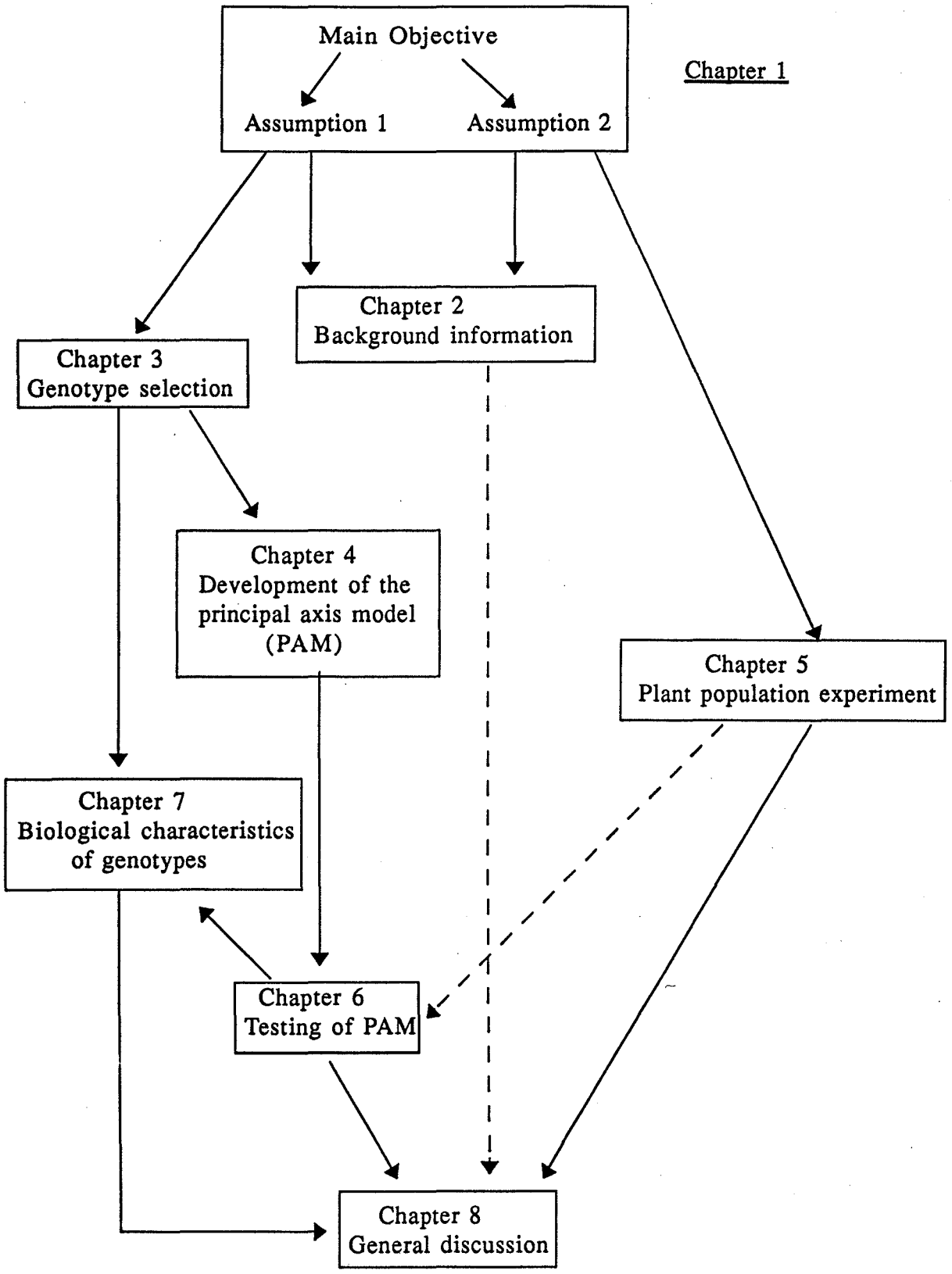
1.3 PROJECT STRUCTURE

This thesis is presented in eight chapters (Figure 1.1). Chapter 2 is a review of the literature on causes and consequences of seed yield variability. Particular reference is made to the techniques available to measure yield and possible causes of yield variability. Chapter 3 outlines the yield structure of six morphologically distinct field pea genotypes selected from a cultivar evaluation trial in a field pea breeding programme. The results from these genotypes are used to test the first assumption (Section 1.2) of a relationship between the seed yield of a crop and its PWT and PHI distributions. Formalizing this relationship into a testable system is addressed in Chapter 4, where a statistical framework for describing the structure of crop yields is developed. This framework is based on the analysis and interpretation of the relationships between SWT and PWT, and the mean and standard deviation (SD) of their frequency distributions. The framework leads to proposals about how changes in these distributions may influence PHI and CHI values, and seed yields.

In Chapter 5, a plant population experiment is described in which the aim was to alter SWT and PWT distributions produced from four genotypes, by deliberately varying the degree of interplant competition. Results from this experiment were analyzed in two ways. In Chapter 5, the interaction effects of genotype and environment on each of the yield components of field peas is assessed along with their heritability and suitability as selection criteria (Assumption 2; Section 1.2). In Chapter 6, SWT and PWT data from this experiment are used to test the empirical model proposed in Chapter 4. In Chapter 7, the biological characteristics of each genotype are considered in relation to their effect on

seed yield variability among crops. In addition, causes of PWT variability within crops are discussed with emphasis on the production of small plants with lower PHI values. Finally, in Chapter 8 the results are drawn together. The variability of seed yields between and within crops is discussed and differences are interpreted in terms of the empirical model. The results from this study are compared to those previously reported in the literature and the practical implications for pea breeding programmes are discussed.

Figure 1.1: Diagrammatic representation of the relationship of each chapter to the main objective and assumptions of this study.



CHAPTER 2

REVIEW OF LITERATURE

2.1 BACKGROUND

The dried pea (*Pisum sativum*) has been a nutritious food source since Neolithic times (Gane, 1985). It was well known to the Greeks and Romans and was developed for consumption in the green state in the 1700s (Lough, 1987). Pea production dates to the beginning of arable agriculture in New Zealand (Jermyn, 1987) and, today, peas rate as the most valuable grain legume exported from this country (Hill, 1991).

In Canterbury, the principal arable cropping region, 70 % of the 30,000 hectares sown in peas are threshed for dry seed production and 30 % are grown for vining and processing (White, 1987). Pea crops provide farmers with a break crop for disease control and improve soil fertility as well as valuable cash returns (White, 1991).

Pea breeding in New Zealand started in the early 1930's and has continued in various forms since then. The first objective of pea breeding programmes has traditionally been for 'defect elimination'. Specifically, early generation material is screened to improve disease resistance, and the second priority is selection for improved yield (Jermyn, 1987). For field peas, yield trials are usually initiated in the F5 or F6 generations and are used to help distinguish between genotypes for inclusion in trials of later generations. Ultimately the breeder aims to release a high yielding, stable cultivar with disease resistance and adaptability to many environments.

There is no lack of yield potential for field peas but a major problem with current cultivars is their yield variability both within and between sites and seasons (Hedley and

Ambrose, 1981; Heath and Hebblethwaite, 1985; Kelly, 1987; White, 1987). This study concentrates on yield variability within field pea crops. Similar problems have been observed in other grain legumes, including lentils (*Lens culinaris*; McKenzie, 1991) and field beans (*Vicia faba*; Thompson and Taylor, 1982). To reduce this variability it is necessary first to investigate the underlying physiological causes, and then to offer breeders appropriate selection criteria for screening genotypes.

Identification of the management, cultivar and environmental factors that cause yield variation in peas is an important research goal. Good crop management advice is available for peas (Jermyn, 1984), but much less is known about environmental influences on the growth and yield of pea crops, or the cultivar characteristics associated with stable, high yield potential (Wilson *et al.*, 1991). As Gallagher *et al.* (1983) indicated, environmental influences usually have much greater effects on crops than management practices. This is especially true for peas. To identify which environmental factors, and genotypic characteristics, most affect yield stability and variability, it is necessary to understand the processes that influence the growth and yield of a crop.

The research reported in this thesis, therefore, aims to identify some of the processes that contribute to yield variability. Once these processes have been identified, crop management techniques and selection strategies in breeding programmes can be developed to reduce their effects. This review of the literature focuses on techniques available for investigation of yield variability, summarises the present state of knowledge, and outlines the research in this study.

2.2 METHODS OF INVESTIGATION

2.2.1 Components of seed yield

In agronomic research, the total seed yield per unit area (TSY) of a grain legume crop is often factored into four yield components:

$$TSY = A \times B \times C \times D \qquad \text{(Equation 2.1)}$$

where A is the number of plants per unit area, B is the mean number of pods per plant, C is the mean number of seeds per pod and D is the mean seed weight (Wilson, 1987). This component approach has been used extensively to describe the yield of grain legume crops (Grafton *et al.*, 1988; Husain *et al.*, 1988; Pilbeam *et al.*, 1991) including both vining and field peas (Stoker, 1975; Falloon and White, 1978; Nichols *et al.*, 1985). These components allow quantitative descriptions of contrasts between lines. Attempts to improve total seed yield have commonly aimed to exploit differences in these components (Krarup and Davis, 1970; Cousin *et al.*, 1985; Singh *et al.*, 1988; Grafton, *et al.*, 1988) with the expectation that high yields would be obtained when each of the components was maximized (Wilson, 1987; Grafton *et al.*, 1988). However, analyses of seed yield based on yield components have also highlighted limitations of this approach. These limitations have resulted from the mutual interdependence, or 'plasticity', among the components and the interaction of genetic and environmental factors on the level of expression of each component.

2.2.1.1 <u>Plasticity of yield components.</u> The plasticity among the yield components is obvious when the effects of changes in plant population are analyzed. Increases in the plant number per unit area usually result in biological yield per unit area increasing towards an asymptote, while total seed yield exhibits either a similar

asymptotic response or a parabolic response (Holliday, 1960a; 1960b; Willey and Heath, 1969; Donald and Hamblin, 1976).

In field peas, Falloon and White (1978) reported an asymptotic response to population for the seed yield of a white pea (Huka) and a parabolic relationship for a Maple pea (Whero). At 25 plants m^{-2} the seed yield of both Huka and Whero was approximately 210 g m^{-2}. However, as the plant population increased from 47 to 163 plants m^{-2}, the seed yield of Huka remained consistent at about 410 g m^{-2}. This consistency was largely due to compensatory reductions in pods per plant from 8.4 to 3.7 and peas per pod from 4.1 to 3.6. The total seed yield of Whero was always less than from Huka, but Whero also showed compensatory decreases in pods per plant and peas per pod as population increased.

Heath *et al.* (1991) reported similar compensatory decreases in pods per plant as population was increased from 20 to 160 plants m^{-2}, resulting in both asymptotic and parabolic yield responses for three semi-leafless field peas.

Other legume crops have also shown compensatory relationships, of decreased pods per plant and seeds per pod with increased plant population, including; chickpea (*Cicer arietinum*; Singh *et al.*, 1988), dry bean (*Phaseolus vulgaris* L.; Bennet *et al.*, 1977; Westermann, and Crothers, 1977; Grafton *et al.*, 1988) and field beans (Husain *et al.*, 1988; Pilbeam *et al.*, 1991).

The plant populations tested in these studies were generally centred around commercially recommended levels. A common finding within each season was the stability of seed yield (as indicated by the asymptotic responses) over the tested range of plant populations (Falloon and White, 1978; Cousin, *et al.*, 1985; Parvez *et al.*, 1989; Heath *et al.*, 1991; Pilbeam *et al.*, 1991). This stability may have resulted from developmental plasticity, whereby yield components are produced in a sequential pattern. When components are

controlled by genetically independent factors, compensation is expected whenever resources are insufficient to maximise two or more components simultaneously (Adams, 1967). For example, the increase in plants per unit area was generally associated with compensatory reductions in other components. The downturn in the parabolic response of seed yield at high populations occurs when the gains from increased plant populations are outweighed by reductions in the product of the numbers of pods per plant, peas per pod, and mean seed weight. The combination of an asymptotic biological yield and parabolic seed yield results in a decreased CHI at high populations (Deloughery and Crookston, 1979; Pilbeam *et al.*, 1991).

Wilson (1987) indicated that this buffered system for yield components limits yield gains from treatments that force changes in a specific yield component. Also, the plasticity of yield components means that yield variability among sites and seasons is usually greater than between agronomic treatments in any one set of circumstances (Wilson, 1987). A further limitation of the components approach to the analysis of seed yield is that it documents differences in terms of changes in components, but cannot predict the seed yield responses to a treatment at different sites or in different seasons (Wilson, 1987; Pilbeam *et al.*, 1990).

2.2.1.2 Response to favourable environments. In favourable conditions all yield components tend to be elevated. For example, Anderson and White (1974) reported that irrigation consistently increased the yield of vining peas. The higher yields were associated with greater numbers of pods per plant and peas per pod at several populations. McNeil (1991) reported that all yield components of *Plantago ovata* increased together as environmental suitability increased. The yield components of spike number and length showed the greatest plasticity and responded to an inherent increase in the yield capacity of the plant, rather than being increased by the action of specific genes. In effect the greater suitability of an environment was reflected by yield component increases, rather than the increase in yield components resulting in the higher yield (McNeil, 1991). This principle probably applies to all seed crops.

2.2.1.3 Genetic analyses of yield components. One fundamental objective of agricultural plant breeding is to increase crop yield. Yield components have often been used as selection criteria because they provide readily definable contrasts between genotypes that are presumed to be associated with yield differences. Therefore breeders have aimed to produce higher yielding cultivars by exploiting variation in these components (Snoad and Arthur, 1973a; 1973b; Singh and Singh, 1970; Chandel and Joshi, 1979).

To exploit variations in these components for yield improvement, it is first necessary to apportion the variations to genetic and non-genetic factors (Jermyn and Slinkard, 1977). There is usually an interaction between the effects of these two groups (Poehlman and Borthakur, 1977) which means that the relative performance of genotypes may change in different environments. Pooled analysis of variance of yields measured in contrasting environments determines the extent of genotype by environment (GXE) interaction and, coupled with broad sense heritability estimates, provides a basis for some separation of genetic and non-genetic components.

The presence of a significant GXE interaction means that genotypes are responding differently to different environments and indicates that stability analysis may be useful for comparisons among genotypes (Finlay and Wilkinson, 1963). Stability across environments may be a desirable property of a genotype intended for use in a wide range of conditions (Singh and Chaundhary, 1985). A large GXE interaction (relative to the genotype effect) and low broad sense heritability estimate for a character indicates that progress in yield improvement through direct selection for that character is probably not feasible (Samad, 1988). If this occurs for all yield components then alternative methods for discriminating between genotypes must be found.

Broad sense heritability estimates for a component allow separation of variability into additive and non-additive effects. If additive effects exist, and they are correlated with

yield, it may be possible to exploit the component for yield improvement. However, the inability to extrapolate results of inheritance studies beyond the parents used in the experiment, and the frequent occurrence of large GXE interactions, has caused doubt about the effectiveness of managing or selecting yield components to increase yield (Snoad and Arthur, 1973a; 1973b; Wilson, 1987).

The results from studies of the mechanism of inheritance for number of peas per pod can be used to demonstrate the variability between parents. Krarup and Davis (1970) reported that crossing resulted in an increased number of peas per pod, but Singh and Singh (1970) observed a reduction. Snoad and Arthur (1973a; 1973b) found both increases and decreases. Studies of the nature of genetic control of number of peas per pod have shown that additive effects are more important than non-additive ones (Gritton, 1975; Kumar and Agrawal, 1981), and non-additive variance greater than additive variance (Dubey and Lal, 1983).

In a review on the inheritance of reproductive characters in peas, Samad (1988) reported important additive and non-additive effects for numbers of pods per plant, peas per pod, and mean seed weight. From a full 5X5 diallel experiment and analyses of GXE interactions, Samad (1988) concluded that number of pods per plant had a low genotypic effect, and low heritability estimates. This meant that yield would respond slowly to direct selection for this character. Furthermore, Samad (1988) considered that mean seed weight was unstable and could not be relied upon for direct yield improvement across environments.

The poor predictability and uncertainty of the value of results from agronomic and breeding strategies based on yield components analyses have led to the development of alternative methods for investigating variability of crop growth and yield. These approaches have aimed to quantify relationships between crop performance and environmental factors, by creating models with a sound physical and physiological basis that can be used to interpret and analyze experimental results.

2.2.2 Crop Models

Crop simulation models provide a rational, quantitative basis for analysing and interpreting the results of agronomic research. A principal objective of crop models is to allow information from one site and season to be used to predict crop performance for other sites and years. Models have been developed for interpreting experimental results, identifying research priorities and helping to set research objectives, and defining crop responses to environmental and management factors.

2.2.2.1 Model development. The level of detail required within a model depends on its objectives. Whistler *et al.* (1986) suggested that models developed for the prediction of crop yield should include processes at the plant and possibly organ levels of organisation in the biological hierarchy, but that inclusion of processes below these levels is not necessary. Models are often described as empirical or mechanistic although most are a mixture of the two. Empirical models consist of correlative relationships between variables, without accounting for causal relationships in terms of underlying physical or physiological processes (Reynolds and Acock, 1985). In contrast, mechanistic models represent an attempt to describe causality between variables. Mathematical functions are used to represent the known or hypothesized mechanisms for the creation of changes in the variables of the models. Mechanistic models therefore become progressively more realistic as comprehension of the underlying physical and physiological processes develops.

Couched within the development of crop simulation models are cautions from Passioura (1973) and de Wit (1982). They suggest that biological simulation should be considered primarily as a work of art rather than science because it usually fails to meet the expectations of biologists. While acknowledging these concerns, Ritchie (1990) considered there was sufficient evidence that simplified approaches to simulation of particular aspects of crop production was good science. He referred in particular to the

success of simulation at the whole plant and crop level. For example, both the use of accumulated thermal time as a basis for predicting plant development, and the use of the amount of solar radiation intercepted to predict biomass accumulation have been successful aspects of crop modelling. However, Ritchie (1990) also pointed out that a major problem limiting the creation of better crop models has been the poor understanding of the partitioning of biomass to the growing organs of plants.

2.2.2.2 Plant based models for yield prediction. When a model is used for predicting the seed yield of a crop, the ability to predict biomass accumulation and its partitioning to economic yield are crucial features of the model. Two principal approaches have emerged for simulating biomass accumulation and partitioning. The more mechanistic approach uses the plant as the basic unit. It involves calculation of gross canopy photosynthesis based on the amount of solar radiation intercepted each day and on radiation use efficiency. The gross canopy photosynthesis is a function of radiation availability and the total photosynthetic area of a plant while the radiation use efficiency is a function of the carbon dioxide assimilation rates of individual leaves (Ritchie, 1990).

This first approach requires input information on the specific leaf weight, the mean daytime air temperature, and estimates of maintenance and growth respiration. The partitioning of dry matter to grain is dependent on source-sink relations in a diverse and detailed but empirical manner, with some dependency on the crop in question. Output values are generally predicted for the average plant in a crop, and then accumulated for all individuals in the population to generate crop values.

This approach has been used in the development of the 'CERES' family of models for several crops (Ritchie, 1990) including wheat (*Triticum aestivum*), maize (*Zea mays*), millet (*Panicum miliaceum*), rice (*Oryza sativa*) and sorghum (*Sorghum spp.*), as well as in 'SORKAM' for grain sorghum (Rosenthal *et al.*, 1989), and 'CORNF' for maize

(Stapper and Arkin, 1980). Models that utilize this approach give a dynamic prediction of seed yield accumulation based on a changing estimate of CHI throughout the growth period of a crop.

A major problem with complex mechanistic models is the amount of resources required to provide input data. Ritchie (1990) suggested attempts should be made to define a minimum data set to allow wider utilization of models. Following on from this would be the development of generic models which specific modules could be added to or removed from as conditions change. The predicted seed yield from a crop simulation model could then become an input module for economic or political models (Ritchie, 1990).

Models have been developed for most of the major arable crops particularly cereals and high value legumes including soybeans, (*Glycine max*) lucerne (*Medicago spp.*) and peanuts (*Arachis hypogea*) as outlined in Table 1 of both Whister *et al.* (1986) and Ritchie (1990). However, no simulation model has been developed for the prediction of seed yield for pea crops, although physiological research at the organ and whole plant level has provided some insight into the dynamics of dry matter distribution in pea plants. For example, Pate and Flinn (1973) have shown that less than 2 % of the $^{14}CO_2$ supplied in the vegetative growth phase (Knott, 1987) was eventually transferred to developing seeds. In contrast, a 76 % transfer of the ^{14}C-photosynthate formed during the reproductive phase (Knott, 1987) was supplied to seed. Furthermore, Pate and Flinn (1973) showed that the contribution of carbon accumulated from leaflets to the subtended fruit (up to 75 %) is consistently greater than from stipules (10-20 %) in conventional plant types. More recent work has seen the construction of models to examine the water, carbon, and nitrogen use of a developing seed throughout its growth (Pate *et al.*, 1977; Pate, 1985).

2.2.2.3 Crop based models for yield prediction. An alternative modelling approach for predicting biomass accumulation and seed yield is based on an assumption of constant efficiency of conversion of intercepted radiation to dry matter (DM) at the whole crop level of organisation. The hypothesis underlying models based on this principal is that the growth of a crop with adequate water and nutrients, and free from weeds, pests and diseases, is related linearly to the amount of photosynthetically active radiation (PAR) intercepted during active growth (Monteith, 1977):

$$C = E\ Q \qquad \text{(Equation 2.2)}$$

where C is the rate of above-ground dry matter production, E is the efficiency with which PAR is converted to DM, and Q is the amount of PAR intercepted by the canopy.

This approach has been extended to predict seed yield as the integral of the growth rate with time multiplied by the harvest index (Monteith, 1977):

$$TSY = CHI\ C \int dt. \qquad \text{(Equation 2.3)}$$

This more functional approach to the prediction of biomass accumulation and partitioning has been used successfully to describe the growth of several crops (Biscoe and Gallagher, 1977; Monteith, 1977; Gallagher and Biscoe, 1978; Charles-Edwards, 1982), and has been extended to analyses of the yields of pea crops in New Zealand (Jamieson *et al.*, 1984; Wilson *et al.*, 1985). This approach satisfactorily described the seed and biological yields of pea crops in a wide range of conditions, even though seed yield varied considerably between sites, seasons, cultivars, sowing times and irrigation treatments. Wilson (1987) summarized the main conclusions from the studies on peas:

1) Yield variations were associated with changes in all four parameters (E, Q, CHI, C dt).
2) The value of E was usually consistent at about 2.4 g of DM per MJ of PAR intercepted (irrigation affected this in one treatment).
3) CHI varied among treatments.
4) Differences in total biological yield were caused mainly by variations in the duration of growth and the consequent differences in the amounts of PAR intercepted.

From these conclusions Wilson (1987) suggested that crop management methods should aim to maximize the duration of growth, and consequently maximize biological yield, provided the duration of seed fill is not restricted and that CHI remains high.

Heath and Hebblethwaite (1987) used a similar approach for analyses of genotypes with conventional, semi-leafless and leafless plant types. Based on photosynthetic area indices, they concluded that values of E were consistent at 1.90 g DM per MJ of PAR for Øyjord-drilled plots and 1.65 g DM per MJ of PAR for precision crops, regardless of the plant types.

2.2.3 Simulations of Dry Matter Partitioning in Crop Models

Crop simulation models can be used to predict the biological yield of crops with reasonable accuracy. However, the prediction of CHI and therefore the seed yield of a crops, has been more difficult, particularly when crops experience water stress (Ritchie, 1990). This difficulty relates to the inability to simulate accurately the mechanisms of dry matter partitioning as it occurs during crop growth. For example, Jamieson et al. (1991) comment that when the 'ARCWHEAT' model, (Weir *et al.*, 1984; Porter, 1984), developed in the United Kingdom, was tested on wheat crops grown in New Zealand the simulation of phenological development, and biomass accumulation was very good while

predictions of grain number and mean grain biomass was poor. The simplest empirical approach employed by Monteith (1977), is to apply a single CHI value and use it as a partitioning coefficient throughout growth. A more complex but equally empirical approach is to alter the partitioning coefficients during growth. The accuracy of the seed yield prediction therefore depends on the accuracy with which the partitioning of dry matter and coefficients for CHI have been estimated.

A common problem for grain legume crops is the variability in harvest index between crops and seasons. For example, in chickpea, Hernandez (1986) reported CHI values of 0 % in a wet season and 45 % in a drier season. For field beans, Attiya (1985) calculated CHI values of 46 % for one year and 20 % for the next.

The lack of capability to simulate dry matter distribution and therefore predict CHI in crop models suggests that this is an area requiring further research. Thus, model development has helped to identify harvest index variability as an important research priority.

2.2.3.1 Variability within crops. Defining a single partitioning coefficient may be a suitable method for estimating CHI in cereals and other crop species with extensive domestication, where the range of individual PHI values is relatively low. However, it may be less accurate for unimproved or less domesticated species where a wide range of PHI values within crops can be found (Ambrose and Hedley, 1984; McNeil, 1991). There is evidence from analyses of yield components and dissections of populations on a per plant basis, that variability among plants in a crop may influence seed yield for some crop species. Thus, the average plant may not be a good indicator of the overall performance of plants within a crop. This is particularly likely in grain legume crops. For example, Kirthisinghe (1986) found PHI values that ranged from less than 10 % to over 60 % in a crop of lentils. The extent of variability within crops is difficult to assess because data on the performance of, and variability among individual plants within agricultural crops is scarce.

2.2.3.2 Variability in field pea crops. Variability among plants has been proposed as an important cause of low and unstable yields in field pea crops. Hedley and Ambrose (1981) sampled a 1 m^2 area from a commercially grown field pea crop and found 30 % of the plants were barren (PHI = 0 %). They also found that the smaller plants in the population tended to have lower PHI values than the larger plants, and that the maximum PHI, of about 60 %, was similar to PHI values from spaced plants grown free of interplant competition.

Following these observations, Ambrose and Hedley (1984) conducted experiments with uniform planting patterns and pre-germinated plants. They compared the levels of variability of PHI and individual PWT among three leafless pea genotypes (Snoad, 1974) at five plant populations (100 to 277 plants m^{-2}). After minimizing agronomic variation, they found that there was a residual level of variability within crops. The PHI values were zero for 60 % of the plants from their lowest yielding genotype with the remainder evenly spread up to a value of 70 %. This range of PHI values resulted in a mean PHI of only 30 % for the crops sown at 277 plants m^{-2}. The CHI range from this low yielding genotype was 30 to 38 % which was about 10 % lower than that from the two higher yielding genotypes. In comparison, the two higher yielding genotypes had similar PHI ranges to the low yielding genotypes of 0 to 70 %, but less than 14 % of their plants were barren. This lower proportion of barren plants resulted in mean PHI values of at least 46 %.

For all three genotypes, the extent of positive skewness in PWT distributions increased with population. The higher populations therefore had greater numbers of small plants with generally lower PHI values. It appeared that the determination of small plants, and therefore the high plant to plant variability within the low yielding genotype, was initiated early in canopy development. Genotypic differences in the potential for partitioning assimilate were small, as shown by the similarity in the maximum PHI achieved (65-70 %) by all three genotypes. Ambrose and Hedley (1984) concluded that yield

improvement in dried pea cultivars was more likely to come from a reduction in the mutual antagonism between individual plants than by improvement in the potential PHI of cultivars. Specifically, they hypothesized that CHI and therefore seed yield could be increased by reducing the proportion of small plants in a population. Furthermore, if a high variance for PHI was a genetically determined character, then it would probably be sensitive to small changes in the environment. Selection by pea breeders should focus on genotypes with uniform PHI distributions (Ambrose and Hedley, 1984).

From these hypotheses, Hedley and Ambrose (1985) attempted to identify the characteristics of a high yielding crop ideotype for field peas, and therefore to define selection criteria for a breeding programme.

2.2.3.3 Yield components. Despite the plasticity among yield components, they have become accepted as useful descriptors of yield for cereals and legumes. Of concern to Husain *et al.* (1988) were observations that the product of plant population and yield components per plant often substantially overestimated the measured yield of field beans (El-Nadi, 1970; Ishag, 1973; Sprent *et al.*, 1977). Pilbeam *et al.* (1991) reported that seed yields calculated from yield components averaged 27.6 % higher than the actual yield from the threshed samples. Conversely multiplication of the yield components of vining peas reported by Stoker (1975) underestimated the observed seed yield by approximately 10 %.

Discrepancies between the measured and calculated seed yield estimates indicate a weakness in sampling techniques. Sample sizes may have been too small to represent the crop population accurately, or the mean values for yield components may not have been representative of the plant population, particularly if the population values were not normally distributed (Benjamin and Hardwick, 1986). Both possibilities suggest that variability between plants may have been greater than expected. It is therefore necessary to estimate the extent of this variability.

2.3 CHARACTERISTICS FOR A FIELD PEA IDEOTYPE

The use of crop ideotypes as a basic approach to plant breeding was first proposed by Donald (1968). This incorporated his previous work (Donald, 1962; 1963) that had suggested plant breeders should consider harvest index, morphological characters that affect the photosynthetic capacity of a plant and the effects of competition in the assessment of early generation material. Donald (1968) proposed that successful crop ideotypes would be weak competitors relative to their mass. These ideotypes would therefore make a minimum demand on the resources per unit dry matter, and compete to a minimum degree with neighbouring plants in a crop community. In a review of the ideotype concept for plant breeding Sedgley (1991) concluded that this approach, based on the definition of weak competitors, had potential for defining the characters of high yielding cultivars of new crops in new environments.

For field peas Ambrose and Hedley (1984) hypothesized that vigorous or highly competitive field pea phenotypes may have the most variation in PHI when grown in crop communities with a few dominant plants contributing the majority of the seed yield. Many small plants with low PHI values would also be present, and consequently the CHI would be low. They suggested that for a field pea crop to produce stable, high yields, it may be best for most of the individual plants in the community to be weak competitors. Although these individuals may exhibit poor performance as single plants, they may also produce more uniform PHI values when grown in a community.

Ambrose and Hedley (1984) extended their discussion to suggest that a preferred field pea ideotype should be: non-branched or late branching (so that interplant competition would suppress development of branches), relatively early flowering (so that assimilate was partitioned into reproductive structures when competition between plants was low), indeterminate in habit (to increase the duration of assimilate partitioning to seeds and therefore reduce competition between yield components), have a single pod at each

reproductive node, and have seeds with a low demand for assimilate per unit time. Snoad (1985) agreed with these characteristics but also suggested that improved stem strength and therefore standing ability was required. Cousin *et al.* (1985) suggested spring pea cultivars should be moderately short with few branches, a small leaf area and large seeds. Ideally, plants in a crop would be planted in uniform patterns to allow similar amounts of growing space and minimize competition between plants (Ambrose and Hedley, 1984).

The introduction of the recessive genes 'afila' (*af*) and 'stipule-less' (*st*) to produce the leafless (*afaf:ststst*) and semi-leafless (*afaf:StSt*) plant types (Snoad, 1974) has expanded the range of phenotypes available for selection and evaluation in breeding programmes. Each of these plant types could form the basis of the ideotype proposed by Ambrose and Hedley (1984). Since the introduction of the leafless and semi-leafless phenotypes, comparative agronomic studies have been undertaken between these and conventional phenotypes and have identified some general characteristics of each plant type.

2.3.1 Leafless Phenotypes

The introduction of leafless field pea genotypes was expected to improve yields by reducing lodging and, possibly, disease incidence through the improved standing ability and canopy ventilation provided by the greater number of tendrils (Hedley and Ambrose, 1981). After trials to compare the performance of leafless and conventional pea crops, several problems were highlighted. The leafless genotypes had poor light interception, and therefore lower biological yields than conventional peas at the same population. When leafless peas were sown at higher plant populations, to increase light interception, the CHI decreased and potential gains in seed yields were not realised. Comparisons of growth rates with semi-leafless and conventional types showed that leafless peas had reduced absolute and relative growth rates (RGR) partly due to poor light interception and poor carbon fixing efficiency by the tendrils (Snoad, 1981; Pyke and Hedley, 1985). In addition, these stipule-less lines appeared more susceptible to *Aschochyta* and downy

mildew (*Personospora viciae)* infections, and were found to be poorly adapted to conditions in France (Cousin *et al.*, 1985). Furthermore, it was from leafless genotypes that Ambrose and Hedley (1984) found the diverse range of PHI values within their lowest yielding genotype (Section 2.2.3.3). Attempts to increase yields by enlarging the stipule of leafless genotypes resulted in thicker but weaker stems and larger seeds but had little effect on yield. From these observations Snoad (1985) concluded that a reduction in the size of stipules on the semi-leafless genotypes may be the preferred strategy to improve field pea crops.

2.3.2 Semi-leafless Phenotypes

By replacing the *st* gene with *St*, the agronomic advantages expected from the leafless phenotype have reportedly been retained along with similar growth rates to conventional genotypes (Snoad, 1981; Pyke and Hedley, 1983). It was, therefore, suggested that semi-leafless peas could be sown at populations that enable high light interception without adversely affecting CHI. Cousin *et al.* (1985) reported seed yields from semi-leafless genotypes was equal to or 10-20 % higher than conventional plant types, even though the green leaf area was reduced by 40 %. The yield increases obtained with the semi-leafless lines were attributed to an even distribution of leaf area along the stem, especially at the fertile nodes, and less interplant competition than in conventional types. These factors may have allowed better light penetration through the canopy and therefore enhanced stipule activity, and made extra assimilates available for transfer to seeds.

Furthermore, Heath *et al.* (1991) found that for three semi-leafless cultivars the optimum yields were obtained from plant populations of 70 to 140 plants m^{-2} which were similar to those required for conventionally leafed peas.

Overall, semi-leafless genotypes appear to have advantages over the leafless genotype. However, no dissections of populations have been made which would allow comparisons of plant to plant variation within crops of the two types.

2.3.3 Conventional Phenotypes

Low and unstable yields have been identified as problems in field pea crops (Section 2.1), and most of these problems have been in crops with conventional leaf types. Conventional field peas are susceptible to lodging and consequent seed staining and chitting and have a higher susceptibility to disease (Hedley and Ambrose, 1981). Their poor standing ability results from the distribution of foliage and reproductive organs at the tops of plants making them top heavy and unstable.

Conventional plant types may be improved by a reduction in their foliage production or internode length to decrease the amount and effects of lodging (Heath and Hebblethwaite, 1985; Snoad, 1985). Traditionally, conventional plant types have been selected by breeders for superior performance as single plants and those chosen have been competitive and dominant (Donald and Hamblin 1976; Wilson, 1987). When evaluated in long narrow drill plots the yield potential from these vigorous types may be overestimated due to large edge effects (Heath and Hebblethwaite, 1985) and their suitability as crop plants incorrectly reinforced. It is possible that a less competitive conventional genotype may provide the basis for development of an ideotype with uniform PHI for all plants as a primary objective.

2.4 HARVEST INDEX AS A SELECTION CRITERION

2.4.1 Direct Selection for Harvest Index

Many historical advances in grain yield potential of cereal crops can be related to increases in harvest index. For example, in oats (*Avena spp.*), rice and barley (*Hordeum vulgare*) shorter straw has been associated with decreases in the vegetative component of total yield, and may have reduced intraplant competition for assimilate, thus permitting greater ear growth (Donald and Hamblin, 1976). However, Donald and Hamblin (1976) suggested that plant breeders have not purposely sought an increase in harvest index. Rather, the increase has arisen as a secondary effect of other selection criteria. Donald and Hamblin (1976) advocated higher harvest index as a direct selection criterion in preference to selection for yield, particularly in cereals.

In a review of results from selections based on harvest index, Snyder and Carlson (1984) reported positive correlations between grain yield and harvest index for barley, oats, wheat, soybeans and pigeon pea (*Cajanus cajan*). Most results showed that selection for harvest index resulted in higher yields than direct selection for grain yield. However, results from selections based on either harvest index or grain yield are not necessarily transferable across seasons or environments, because of high GXE interactions. The effectiveness of selections over a wide range of conditions has therefore been questioned (Deloughey and Crookston, 1979; Johnson and Major, 1979; Whan *et al.*, 1981; Snyder and Carlson, 1984).

For wheat, selection for harvest index at low populations has been suggested as more efficient than selection for grain yield (Fischer and Kertesz, 1976). In contrast, Nass (1980) reported that indirect selection for improved seed yield, based on improved harvest index in wheat, was more efficient at near-commercial plant populations than for spaced plants. Ambrose and Hedley (1984) suggested that these contradictory results (from

Fischer and Kertesz (1976) and Nass (1980)) may have been caused by the relatively small effects on PHI variability within crops of interplant competition in cereals when compared with their findings of large differences between field pea plants. For field peas, Jermyn (1976) considered that harvest index was valueless as a selection criterion and Samad (1988) supported this finding.

Other investigations of harvest index, to provide information for crop simulation models or selection criteria for breeding programmes, have been based on studies of empirical relationships between the components of harvest index, namely SWT and PWT.

2.4.2 Relationship Between SWT and PWT

Strong linear relationships between seed weight and plant weight per unit area have been reported for many crops. These include maize (Voorhees *et al.*, 1989; Prihar and Stewart, 1990; Sinclair, *et al.*, 1990), sorghum, (Olson, 1971; Unger and Jones, 1981; Prihar and Stewart, 1990) and faba beans (Pilbeam *et al.*, 1992). A similar relationship has also been found on a per plant basis for maize (Gardner and Gardner, 1983), sorghum (Gardner and Gardner, 1983; Prihar and Stewart, 1991) and field peas (Hedley and Ambrose, 1981). Gardner and Gardner (1983) suggested that a linear relationship was also appropriate for many different species of grain crops and for cotton lint and seed.

The relationships take the form $S = a + b \times P$, where S and P represent the seed and plant weights respectively on either a per unit area or per plant basis, and a and b represent the y-axis (S) intercept and slope of the linear regression respectively. Gardner and Gardner (1983) indicated that for individual plant data, where S is the SWT and P is the PWT, the intercept of this line may be negative. This can be interpreted to infer that a minimum plant weight (MPW) may exist for seed production. Furthermore, Gardner and Gardner (1983) suggested that the MPW for sorghum and other small grain crops would be lower than for larger grained crops such as maize. The value may be very small for wheat and

barley because their regression lines almost passed through the origin (Gardner and Gardner, 1983). If the line does pass through the origin then the PHI would be constant and equal to the slope of the regression line regardless of the PWT. This means that even the smallest plants are partitioning a similar proportion of their PWT to SWT. Under these circumstances, selections based on the SWT versus PWT relationships become the same as those based on CHI. This may explain the greater value of harvest index as a selection criterion in small grain crops (Nass, 1980) than in crops such as peas with larger seeds (Jermyn, 1976).

Extrapolations of the data presented by Hedley and Ambrose (1981) indicate a MPW of about 1.0 g of DM per plant or about 15 % of the mean PWT, from a commercially grown pea crop. Although the idea of a simple linear regression between SWT and PWT seems to be widely accepted, the existence and interpretation of the importance of the MPW is a matter of uncertainty.

2.4.3 Genetic Harvest Index (GHI)

Prihar and Stewart (1990) hypothesized that although harvest index is controlled genetically it is also influenced by the environment to such an extent that intercultivar comparisons are difficult. In particular, they proposed that the reactions to stresses may differ among cultivars. Therefore, harvest index values obtained under conditions of stress may favour cultivars that could be out-performed in low stress or stress free conditions. Prihar and Stewart (1991) suggested that a genetic harvest index (GHI) should be established and used as the basis for comparisons among cultivars and for assessing environmental effects on harvest index. Central to their method for determining a GHI was the idea that a MPW does not exist and that its calculation by Gardner and Gardner (1983) was an artefact of the inclusion in the regression analysis of plants grown under stress. Consequently, Prihar and Stewart (1990) suggested that harvest index was independent of the mature PWT but possibly varied between environments.

For maize, wheat and sorghum, the GHI was estimated by plotting a line through the origin and points from crops with the highest CHI for a particular cultivar. This line was described as the upper bound, or potential harvest index, and its slope was used to represent the GHI (Prihar and Stewart, 1990). This method was suggested as the basis of a procedure for comparing crop species or cultivars for their ability to partition assimilates to grain under given environmental conditions. It could also be used as the base from which the effects of environmental stresses could be quantified.

The data presented by Prihar and Stewart (1990) was taken from crop results and therefore estimated a GHI at the whole crop level. This approach was then used in the same manner to examine data for individual sorghum plants (Prihar and Stewart, 1991). These regression analyses of SWT against PWT produced positive, zero and negative coefficients for the SWT axis intercepts. The positive coefficients were explained as impossible values that were artifacts which resulted from larger plants with lower PHI values reducing the slope of the regression line. Negative coefficients were considered to result from the inclusion of small plants with low PHI values obtained from high plant population treatments, with consequently higher levels of interplant stress.

Prihar and Stewart (1991) emphasized that the concept of a MPW arose from the combining of data from stressed and non-stressed crops. They concluded that their results did not support the existence of a MPW in stress free environments, and that the slope of the upper-bound GHI line was dependent on environment. Therefore, comparisons of cultivars across locations was not valid.

A common theme in the literature on harvest index is the variability in CHI values between sites and seasons. In addition, the use of the generic term harvest index by most authors, without distinction between CHI and PHI, indicates that differences between these two terms have been considered insignificant, or not considered at all. However, the variability in PHI values within grain legume crops implies a need for a distinction between CHI and PHI when seed yield differences are being investigated. The tendency

for small field pea plants to have lower PHI values, and the proposal that improved yield may come through the selection of field pea plant types that result in uniform PHI distributions (Ambrose and Hedley, 1984), indicates that variability of PWT and PHI values within crops should be examined.

2.5 VARIATION IN PLANT POPULATIONS

In a major review of the variation in PWT within even-aged stands of monocultures, Benjamin and Hardwick (1986) identified two problems: 1) How should PWT variation be described statistically ? and 2) How can the causes of variation be isolated for investigation ?

2.5.1 Statistics for Quantifying Variation

The frequency distribution is commonly used to display data from a population of individuals such as plants in a crop, and is summarized by measures of location and dispersion. Location statistics describe the position of a distribution and include the mean, median and mode. Dispersion statistics such as the range, standard deviation (SD) and variance give some quantification to the spread of values around the location statistic (Sokal and Rohlf, 1981).

The mean and SD contain all the information about a normally distributed population. The coefficient of variation (CV) then provides a useful, dimensionless parameter for comparisons between populations when the SD value varies with the mean (Sokal and Rohlf, 1981). The CV for PWT values have been reported to range from 10 % in widely spaced genetically identical maize crops (Edmeades and Daynard, 1979) to 200 % in high density crops with non-normal frequency distributions (Benjamin and Hardwick, 1986). The nature of departure from normality can be expressed using measures of skewness (or asymmetry) and kurtosis, which then need to be considered with the SD or CV.

Within a crop, the frequency distribution for PWT values has been found to be approximately normal at, or shortly after, seedling emergence. Distributions tend to become positively skewed as time passes and interplant competition becomes progressively more significant (Koyama and Kira, 1956; Ford, 1975; Naylor, 1976). However, Turner and Rabinowitz (1983) also found positively skewed distributions, in which there are many small and few large PWT values, in non-competing *Festuca paradoxa* populations.

In skewed frequency distributions one tail is drawn out more than the other so that the mean and median values do not coincide (Sokal and Rohlf, 1981). In ecological literature positively skewed distributions are said to exhibit hierarchy (Ford, 1975; Waller, 1985; Weiner, 1985). The positively skewed population may become bimodal, with a two-tiered canopy of large and small plants, with subsequent self-thinning of the small plants (Westoby, 1984) that ultimately causes the population to become unimodal and again approach a normal distribution (Ford, 1975).

However, Ford (1975) indicated that a positively skewed distribution may be generated in several ways, and that the distribution for the weight of objects is dependent on the product of the object's three linear dimensions and its density. If the linear dimensions are precisely normally distributed then the triple product approaches positive skewness and may simply reflect a normal distribution of plant height (Ford, 1975; Mead, 1979) or result from genetic variation in individual growth rates (Koyama and Kira, 1956; Hara, 1984; Bonan, 1988).

Kurtosis, or peakedness, can also be used to describe frequency distributions. Leptokurtic distributions have more values near the mean and tails than normal distributions. Platykurtic distributions have more values in the intermediate regions then at the mean or tails (Sokal and Rohlf, 1981). Calculations of skewness and kurtosis involve moment statistics, which are generally designated g_1 and g_2 respectively and can be tested for significance using Students 't' tests (Sokal and Rohlf, 1981). A negative g_1 value

indicates skewness to the left, and a positive g_1 indicates skewness to the right. A negative g_2 indicates platykurtosis while a positive g_2 shows leptokurtosis (Sokal and Rohlf, 1981).

These summary statistics provide the tools for describing variation in a population. The second problem considered by Benjamin and Hardwick (1986) was the isolation of possible causes of plant to plant variation within crops. Benjamin and Hardwick (1986) approached this problem by separating causes into pre-emergent and post-emergent sources.

2.5.2 Pre-emergent Sources of Variation

Variation between seeds in their weight, the size of the embryonic axis and several other characters, collectively referred to as seed vigour, may cause differences in pre-emergence growth rates (Hedley and Ambrose, 1985; Benjamin and Hardwick, 1986). Most of the variation in seedling weight shortly after emergence has been related to differences in the duration of pre-emergent growth. This duration may also be affected by extrinsic factors such as sowing depth and variation across the seed bed for factors such as soil impedance, moisture availability and temperature (Emerson and Minor, 1979; Benjamin, 1990; Wade *et al.*, 1991). Shanmuganathan and Benjamin (1992) showed that increased sowing depth delayed seedling emergence and reduced relative growth rates of spring cabbage seedlings (*Brassica oleracea*). The reduced seedling growth was associated with low light interception by small cotyledons, which resulted from the low partitioning of assimilates to cotyledons during pre-emergence growth in favour of greater hypocotyl length.

The on going effects of delayed emergence were highlighted in an experiment with mixed stands of *Scrophularia nodosa* (figwort) and *Digitalis purpurea* (foxglove) by Van Baalen *et al.* (1984). In their experiment, a one day delay in emergence of foxglove relative to

the figwort (a rosette forming plant) resulted in a 28 % reduction in yield per plant compared to a 5 % reduction for figwort (a stem forming plant) in the reverse situation. From a set of replacement series experiments using barley and fat hen (*Chenapodium album*), Elberse and de Kruyf (1979) concluded that barley out-competed fat hen if the difference in sowing dates was less than 15 days. However, fat hen out-competed barley if sown more than 15 days before barley.

2.5.3 Post-emergent Sources of Variation

After emergence, plants are subject to macro and micro environmental differences, and inherent differences in RGR that all contribute to variation in final PWT and PHI values. However, a general finding has been that the ranking in PWT established at emergence changes little from then on, although smaller plants may have a persistently lower RGR than larger plants (Ross and Harper, 1972; Soetono and Donald, 1980; Benjamin and Hardwick, 1986).

Differences in PWT established at emergence tend to be accentuated by the early emerging plants acquiring a disproportionate share of resources. The late emerging plants tend to become the smallest in a population (Benjamin, 1990). Other factors such as a longer duration of growth for early emerging plants or other intrinsic and environmental factors may result in lower RGR of late emerging plants. The range of emergence dates and size of seedlings at emergence results in differences in seedling PWT at the onset of interplant competition. The interplant competition accentuates the differences between plants to become a major source of variation in the PWT of mature plants (Benjamin, 1990). Benjamin and Hardwick (1986) indicated that the RGR of an individual plant was influenced by its own mass, the space available for growth and the activity of neighbouring plants.

2.5.3.1 Space available for growth. Generally, zones of influence have been used to define the space available to a plant. These zones have been considered as non-overlapping or overlapping (Benjamin and Hardwick, 1986). Defining the space available for plants in a population and optimising the size and shape of this area led researchers to investigate the effects of planting pattern on yield, in an attempt to model this zone of influence. Pant (1979) considered the theoretical implications for yield of different planting patterns and concluded that if the influence zone of an individual plant was plate-like, cylindrical or hemispherical, but not overlapped, the maximum yield showed a dependence on pattern. Greater seed yields were then expected from a regular hexagonal planting arrangement than a square arrangement which, in turn, would be expected to produce a greater seed yield than the common rectangular arrangement.

Variation between plants tends to decrease as planting pattern becomes more uniform (Rogers, 1977; Ambrose and Hedley, 1984) with yield losses very likely whenever plant numbers are inadequate (gaps) or excessive (clumped) (Wade, 1990). For peas, Davies *et al.* (1985), indicated that yield increases as the spatial arrangement approaches 'on-the-square' planting, although Heath and Hebblethwaite (1987) concluded precision drilling by machine is unlikely to increase yields provided crops are sown at sufficient density to ensure satisfactory PAR interception during the reproductive phase.

Mead (1966) used a method of non-overlapping polygons of different shapes and sizes to quantify the zone of influence for each plant in an irregularly spaced carrot crop, and explained up to 20 % of the size variation between individual plants by this method. However, correlation between space and PWT within an agricultural crop is rarely very large (Brewster and Salter, 1980; Breeze and Milbourn, 1981). The RGR, plant height or PWT of an individual plant may vary with space available for growth, but could also be influenced by the size or activity of neighbours (Ford, 1975; Benjamin and Hardwick, 1986; Sutherland and Benjamin, 1993). This is equivalent to saying that it is much more common for overlapping rather than non-overlapping zones to exist in crops.

2.5.3.2 Interplant competition. When the immediate supply of a single factor necessary for growth falls below the combined demands of the individual plants, competition among plants begins within a crop (Donald, 1963). To investigate the performance of individual plants within communities many models of neighbourhood effects have been developed. These have been based on the area of overlap (Bella, 1971), the relative size and proximity of neighbours (Waller, 1981; Weiner, 1984), and the competitive effects of overtopping of small plants by larger plants (Ford and Diggle, 1981; Cannell *et al.*, 1984; Hara, 1986).

In particular, investigations have focused on the relationships between size hierarchies (e.g. positively skewed PWT distributions) and interplant competition. Cannell *et al.* (1984) indicated that competition was a stochastic process where the success of an individual was based on the probability of having smaller neighbours. With plants of different sizes initially randomly dispersed in a plant stand, some small plants will prosper because they have small neighbours while some larger plants will be suppressed by larger neighbours.

2.5.3.3 Asymmetric versus symmetric plant competition. The effects of interplant competition on size hierarchies depend on the nature of the competition. Greater inequality or positive skewness in the PWT distribution has frequently been reported at high populations (Koyama and Kira, 1956; Ford, 1975; Naylor, 1976; Waller, 1985; Petersen *et al.*, 1990). However, the mechanisms proposed to explain these observations have varied. Asymmetric or one-sided competition, by which large plants decrease the RGR of smaller neighbours but not vice versa, has been proposed as the source of these hierarchies (Naylor, 1976; Ford and Diggle, 1981; Weiner, 1988), particularly when competition is for light (Hara, 1986; Weiner and Thomas, 1986). As competition intensifies at higher populations, small plants are suppressed and the RGR becomes positively correlated with PWT. Cannell *et al.* (1984) found that asymmetric competition was the mechanism responsible for evenly dispersed dead trees and positively

skewed frequency distributions for a 7 year old stand of *Picea sitchensis* (Sitka spruce) and a 5 year old stand of *Pinus contorta* (lodgepole pine). Miller and Weiner (1989) modified this idea to indicate that increased PWT variability was caused by asymmetric competition only if plants were grown in a uniform spatial arrangement.

Weiner *et al.* (1990) found that PWT variability of uncrowded dwarf marigold (*Tagetes patula*) populations remained low throughout the growth period, with no evidence of a relationship between initial PWT and subsequent growth. Proportionally all plants grew about the same amount, despite differences in their initial size. In contrast, for crowded plants the ranking of PWT was similar at 3 weeks and at 11 weeks, and PWT variability increased with time. They suggested that this variability further supported the idea of asymmetric competition in crowded populations. However, Weiner *et al.* (1990) also recognised that if competition was completely asymmetric, the largest individuals in crowded populations should be as large as those from uncrowded situations. However, the largest plants in the competitive environment were only 13.4 % of the average PWT of uncrowded plants. Weiner *et al.* (1990) therefore proposed that investigations into plant competition should include information from the uncrowded populations as a genotypic and environmental baseline for understanding competition.

Weiner (1985; 1988) concluded that if competition was symmetric, that is there was even or two sided competition, resources would be shared in proportion to PWT. Variability in PWT would therefore not increase as the intensity of competition increased. Symmetric competition has been incorporated into models of zones of influence developed particularly in forestry studies (Opie, 1968; Bella, 1971; Daniels, 1976). Taken together, the data of Weiner (1988) and Weiner, *et al.* (1990), suggest partial asymmetry within the populations.

Bonan (1988; 1991) suggested that the aim of distinguishing between the relative importance of asymmetric and symmetric competition (Turner and Rabinowitz, 1983; Waller, 1985; Weiner, 1985; Weiner and Thomas, 1986; Ellison and Rabinowitz, 1989) has not been appropriate for explaining the increased variability in PWT distributions in competitive environments. Positively skewed distributions were presented as evidence of localized neighbourhood competition that would result from either symmetric or asymmetric competition for resources. The growth of a plant is dependent on the number, size and proximity of localized neighbours rather than symmetric distribution among competing plants that would be expected to reduce resources proportionally for all plants (Bonan, 1991), i.e. multiple factors are operating rather than any single explanation.

Petersen *et al.*, (1990) examined seedling stands of *Fraxinus mandshurica* and observed an increase in positive skewness of the PWT distribution as population increased. However, they also found that RGR was independent of PWT, so a positive correlation between RGR and PWT was not necessary to increase PWT variability. Petersen *et al.* (1990) concluded that asymmetric competition may contribute to the development of skewness without any decrease in the mean RGR of small plants relative to large ones. That is, seedlings with small neighbours may grow free of competition for different lengths of time. The RGR of seedlings with the same PWT may therefore not be equal. In essence, Petersen *et al.* (1990) agreed with work by Hara (1984; 1986) that recognised similar PWT hierarchies may result from either a positive relationship between RGR and PWT or variation in RGR of plants with the same initial PWT.

2.5.3.4 <u>Asymmetric and symmetric competition in field peas.</u> Ellison and Rabinowitz (1989) compared the emergence and growth of two field pea genotypes (leafless and leafed) grown both as individual plants and in competitive environments in a glasshouse experiment. At harvest, the leafless (*afaf:stst:tltl*) genotype had developed fewer hierarchical population structures than the leafed (*Af/-:stst:tltl*) genotype. This result supported the work of Ambrose and Hedley (1984) that was reanalysed and

interpreted by Weiner and Thomas (1986) to show that plant type may reduce the extent of asymmetry in crops. In essence, this was the conclusion reached by Ambrose and Hedley (1984) when they recommended the characteristics for a field pea ideotype which formed the basis of this thesis.

Although Ellison and Rabinowitz (1989) reported the creation of size hierarchies in their competitive populations, the relative sizes of the hierarchies were constant over time. This is in conflict with the idea of progressively increasing asymmetric competition by which differences between the size hierarchies increase over time as the interplant competition increases (Hara, 1986; Weiner and Thomas, 1986). Ellison and Rabinowitz (1989) concluded that their observation of symmetric competition at high populations implied that the below ground resources were limiting rather than competition for light. They concluded that their results did not clearly support the dominance of either asymmetric or symmetric competition. They also suggested that the interacting effects of plant architecture and time of emergence on population dynamics required further study.

2.5.3.5 Measurement of interplant competition. Investigations of interplant competition have been restricted by several practical problems. Firstly, although destructive measurements such as sequential harvest through a season allows accurate measurement of plant biomass, they prevent the growth of the same individuals from being examined continually (Weiner *et al.*, 1990). Furthermore, the structure of the community is disrupted (Ford, 1975). Repeated non-destructive measurements such as plant height, leaf area or stem diameter cannot be used to estimate plant biomass, and become difficult to measure when the canopy closes or plants become entangled.

A criticism of simply evaluating PWT classes within frequency distributions has been that the relative positions of individuals are ignored (Mead, 1979). Information about neighbourhood effects is lost. In order to examine variability of plants within crops and

account for the activity and space of neighbouring plants, some combination of destructive and non-destructive measurements may be necessary. Weiner *et al.* (1990) combined destructive harvest data with non-destructive measurements of plant height and stem diameter to improve the usefulness of both data sets.

2.6 CONCLUSIONS

1. Field pea crops can produce high seed yields under favourable conditions. However, a lack of stability in yields between sites and seasons is a problem common to many grain legume crops, including field peas.

2. Analyses of seed yields through assessment of their yield components can be used to describe differences between crops. However, selection in breeding programmes based on any one component has not produced consistent increases in seed yield, largely due to the magnitude of GXE interactions.

3. Computer simulation models provide an alternative method to yield components for analysing the growth and yield of crops. Highly detailed models (e.g. 'CERES' wheat and maize) and the more functional crop based models used by Wilson *et al.* (1985) for investigation of field peas, have identified the distribution of dry matter and the resulting harvest index as an area that requires further research. Furthermore, results indicate that the variability of individual PHI values within crop communities influences the seed yield from field pea crops.

4. Yield improvement in field peas may come from a reduction in mutual antagonism between individuals and therefore improved stability of PHI, rather than improvement in potential PHI. The ideal plant type to achieve this may have poor performance as an individual plant.

5. Direct selection of harvest index for yield improvement has produced varying results that have differed among crop species. Harvest index may have little value as a selection criterion for field peas.

6. Examinations of SWT against PWT relationships have shown that small field pea plants tend to have low PHI values. Existence of a MPW for production of seed is still contentious. Some researchers have suggested that plants from stressed environments have artificially identified the existence of a MPW.

7. Variability in PWT distributions, and the related variability in PHI values, are caused by both pre-emergence and post-emergence factors. These include seed size, seedling growth, and the micro-climate of each plant within the crop.

8. To examine the effects of interplant competition, some estimate of PWT and the location of an individual within a crop, plus the influence of its neighbours is necessary.

2.7 SUMMARY

The overall goal of the investigation described in this thesis is to examine the causes of low and variable seed yield from field pea crops. Previous studies have implicated small plants and variable PHI values as possible factors that influence seed yields. Selection criteria to overcome such problems have previously been discussed but not tested, while direct selection for PHI has been dismissed.

In this project traditional agronomic analyses including yield components analysis and an alternative method for analysing crop yields are evaluated. The latter method attempts to clarify some of the current debate on the relationship between SWT and PWT, the existence or not of a MPW, and the relationship between PHI and PWT. From this base, the effects of interplant competition within a crop are discussed for both uncrowded and crowded populations. Ultimately the aim is to provide practical selection criteria for use in a field pea breeding programme based on improved understanding and reduction of the variability both within and between field pea crops.

CHAPTER THREE

CULTIVAR EVALUATION TRIAL (1988/89)

3.0 INTRODUCTION

The objective of the experiments described in this thesis was to determine whether differences in seed yields among field pea crops was associated with specific morphological characteristics of genotypes. Investigations were based on the hypothesis that:

> in dried pea crops, the frequency distributions for PHI from non-competitive plant types are more uniform with higher mean values than from traditionally selected competitive types (Ambrose and Hedley, 1984).

In this chapter the selection and classification of several morphologically distinct genotypes is described and the following assumptions that underpin the hypothesis are examined:

1) there is a relationship between seed yield per unit area and PHI distributions,
2) distributions of PWT and PHI vary between crops,
3) smaller plants in a crop tend to have the lowest PHI values,
4) there is a linear relationship between the SWT and PWT of individual plants within a crop.

The data presented in this chapter also provides the opportunity to determine whether differences in seed yield among the genotypes was related to morphological and phenotypic differences, although this idea is explored in greater detail in Chapters 7 and 8.

3.1 MATERIALS AND METHODS

3.1.1 Selection of Genotypes

The plant material used for analyses in this study was selected from the F8 genotype evaluation trial included in DSIR Crop Research's (now the New Zealand Institute for Crop and Food Research) field pea breeding programme during the 1988/89 season. The breeding programme was independent of this study and aimed to differentiate between many lines, and therefore plant types, on the basis of their total seed yield. The breeding trial involved two replicates of 60 genotypes planted in 5 m x 1.5 m plots in a Templeton silt loam soil (New Zealand Soil Bureau, 1968; Cox, 1978) on 10 September 1989.

Forty five days after sowing (DAS) while plants were in their vegetative growth phase (Knott, 1987), all 60 genotypes were screened to enable the selection of morphologically distinct genotypes for inclusion in this study. Genotypes were classified based on visual assessment of: leaf type, either conventional (C) or semi-leafless (S); apparent growth vigour, vigorous (V) or low vigour (L); and the uniformity among plants within the crop, either uniform (U) or non-uniform (N). The objective was to choose genotypes representing eight contrasting phenotypic categories (Table 3.1). However, lines were only selected for six of the categories because there were no semi-leafless genotypes classified as non-uniform. Selections were therefore not possible for categories 7 and 8. The six genotypes selected were from a single F progeny that had been derived from five generations of single plant selections. The pedigree of each genotype is given in Table 3.1.

At physiological maturity all plants within a 1 m^2 sample area were hand harvested from each plot of these six genotypes. Measurements were recorded for SWT, PWT, and PHI, from which seed and biological yields, and CHI, were estimated.

Table 3.1: Phenotypic selection characteristics. Eight phenotypic categories, based on three characteristics, were sought for selection from 60 F8 field pea genotypes in a breeders yield trial in 1988/89. *Parental characteristics were the selection attributes of each parent, with those of the female listed first.

Genotype category	Breeding identification	Phenotypic Categories			Parental characteristics
		Leaf type	Level of vigour	Degree of uniformity	
1	DFFR x (Rovar x Fek)	Conventional	High	Poor	- Long double podding, high ovule number - Erect habit, all round desirability
2	Rovar x Fek	Conventional	High	Good	- Seed size and shape - Seed colour, downy mildew tolerance
3	FP_1H x C530	Conventional	Low	Poor	- Triple podding - High ovule number
4	FP_1H(B) x (Rovar x Fek)	Conventional	Low	Good	- Triple podding - Erect habit, all round desirability
5	973 x 77	Semi-leafless	High	Good	- High yield, semi-leafless - High yield, dark green seeded garden pea
6	1033 x 5	Semi-leafless	Low	Good	- High yield, semi-leafless - Downy mildew tolerant garden pea
7	Not selected	Semi-leafless	High	Poor	-
8	Not selected	Semi-leafless	Low	Poor	-

3.1.2 Statistical Analyses

3.1.2.1 Plant harvest index. To describe and compare frequency distributions, plants with a PHI value of less than or equal to 33 % were arbitrarily classified as 'poor performing' (Benjamin and Hardwick, 1986). Poor performing plants that produced no seed, and therefore had a PHI of zero, were also classified as barren. The percentages of poor performing and barren plants were compared between replicates of a genotype, and among genotypes using confidence limits based on the binomial distribution (Sokal and Rohlf, 1981). When there was no significant difference between replicates the results were pooled for the genotype. Binomial distribution confidence limits were then used to compare these pooled percentages among genotypes.

Arcsine transformations are generally recommended for percentage data and are considered necessary when the values within an analysis exceed a range of either 0 to 30 % or 70 to 100 % (Snedecor and Cochran, 1980; Sokal and Rohlf, 1981). Neither the percentage of poor performing plants between replicates nor among genotypes exceeded the 0 to 30 % range. Transformations were therefore unlikely to change the conclusions based on the original data (Snedecor and Cochran, 1980) and were not used.

Mean PHI values were compared between replicates of a genotype using individual plant data and 95 % confidence intervals based on the pooled standard deviation (Sokal and Rohlf, 1981). The CVs are reported as an indication of the dispersion of frequency distributions, with the caution that care is required when interpreting CV values from non-normal distributions (Benjamin and Hardwick, 1986). Median values are reported as an alternative to the mean values as an estimate of location, because they are relevant for non-normal distributions (Sokal and Rohlf, 1981).

3.1.2.2 PWT distributions. The frequency distributions for PWT were analyzed for normality, skewness (g_1) and kurtosis (g_2) using the *'PROC UNIVARIATE'* from the *'SAS'* statistical package (SAS Institute, 1990).

3.1.2.3 Relationship between SWT and PWT. The relationship between SWT and PWT was investigated using linear regression. However, the method of regression analysis requires consideration. An assumption of least squares regression is that the independent variable, PWT in this case, is measured without error or is a set of targeted values chosen prior to the experiment (Berkson, 1950; Sokal and Rohlf, 1981). This assumption is not fulfilled by the PWT data in this trial which does not have predetermined values, and represent a population of plants with continuous, rather than discrete, measurements.

A second form of regression that deals with distributions of data is commonly called the principal axis regression (Sokal and Rohlf, 1981; Moot and Baruch, 1989). Principal axis regression produces a relationship typically involving two continuous variables, distributed according to the bivariate normal distribution (Sokal and Rohlf, 1981; Moot and Baruch, 1989). For example, principal axis regression is useful for calibration between two measuring devices, neither of which is known to have the correct measurement. A functional relationship is therefore produced between two independent variables. Although the SWT and PWT data represent continuous measurements, physiologically the SWT of each plant is dependent on its PWT, while the reverse situation is nonsensical. The assumption of two independent variables in principal axis regression is therefore not met.

Thus, on a statistical basis, neither regression technique is strictly correct for the analysis of the SWT versus PWT relationship. Both Sokal and Rohlf (1981) and Miller (1986) considered the situation of errors in the measurement of both variables. They concluded that, where the aim is the prediction of a dependent variable from an independent variable, least squares regression is the more appropriate technique. Thus, least squares regression calculations were used to determine the relationship between SWT and PWT throughout this study. The SWT was defined as the dependent variable and PWT as the independent variable.

The data from this trial included a large number of barren plants. This group of plants, were located at the lower end of the SWT versus PWT axes, and may complicate regression analyses by causing leverage. The affect of these plants was investigated using analysis of covariance. The regression slopes and intercepts produced from data sets that included and excluded the barren plants from each of the 12 crops were compared. Significant differences in these values were considered indicative of leverage.

3.2 RESULTS

3.2.1 Yield

The seed yield from the 60 genotypes in this trial ranged from 180 to 500 g m^{-2}. However, among the six selected genotypes, no significant differences were found for seed yield ($p=0.786$), biological yield ($p=0.690$) or CHI ($p=0.556$). These non-significant results were due to variability between the replicates for some of the genotypes. For example, the range of means for seed yield over all six genotypes was from 354 to 413 g m^{-2}, for CVN and SVU respectively (Table 3.2). However, the range in seed yield was larger than this for the two replicates of genotypes CLN, CLU and SLU (Table 3.2).

The range of means for biological yield and CHI of the genotypes were also exceeded by differences between replicates. Genotype means for biological yield ranged from 749 to 890 g m^{-2} and mean CHI from 41.7 to 51.2 % (Table 3.2). In comparison, the range of biological yields between replicates for genotype CVU was from 755 to 940 g m^{-2} and the two replicate values for CHI of genotype CLN were 42.2 and 58.4 % (Table 3.2).

In summary, the variability between replicates was often greater than that found among genotypes for seed and biological yields, and CHI.

Table 3.2: Field pea yields. Genotype and replicate results for total seed yield (TSY), total biological yield (TBY), and crop harvest index (CHI) for the six selected genotypes in the 1988/89 cultivar evaluation trial.

Genotype	TSY ($g\ m^{-2}$)			TBY ($g\ m^{-2}$)			CHI (%)		
	Replicate		Genotype mean	Replicate		Genotype mean	Replicate		Genotype mean
	1	2		1	2		1	2	
CVN	356	353	354	769	760	765	46.3	46.4	46.4
CVU	355	381	368	755	940	848	47.0	40.5	43.8
CLN	410	336	373	701	797	749	58.4	42.2	50.3
CLU	366	461	413	685	941	813	53.4	49.0	51.2
SLU	310	421	366	818	927	873	37.9	45.4	41.7
SVU	415	393	404	930	850	890	44.7	46.3	45.5
(Replicate mean)	369	391		776	869		48.0	45.0	
(p level)			0.786			0.690			0.556

3.2.2 PHI Distributions

The PHI frequency distributions from the 12 plots fell into one of three distinct forms, although the classifications were not necessarily consistent for both replicates of a genotype (Figure 3.1).

In the first distribution form, approximately 20 % of the plants were barren and poor performing, although most plants had a PHI above 33 %. An example of this first distribution form is presented in Figure 3.1A using the data from replicate 1 of genotype CVN. Generally, the five treatments classified in this first distribution form had the lowest mean PHI values (33-42 %), the largest coefficients of variation (34.5 - 49.2 %), In addition their poor performance plants represented a higher proportion of the total biological yield than those in the other two distribution forms (Table 3.3). The crops in this first distribution form also had median PHI values that were between 5.6 and 8.2 % higher than their mean values (Table 3.3).

The second distribution form was unique to both replicates of genotype CLU. The majority of plants had a PHI value above 33 % but a second group of plants were barren or had PHI values of less than 5 %. The distinction between these two groups of plants is highlighted in Table 3.3, which shows 15.3 % of the total number of plants were classified as poor performing and that 77 % of these plants were further classified as barren (Figure 3.1B). In total, the poor performing plants represented less than 6 % of the biological yield from genotype CLU (Table 3.3).

An example for the third distribution form is given in Figure 3.1C, using data from replicate 1 of genotype SVU. The plots represented by this third distribution form were significantly negatively skewed ($p<0.01$), with barren plants representing less than 3 % of the total plant numbers and biological yield (Figure 3.1C; Table 3.3). The relatively small number of barren plants was reflected in lower CV values for PHI, which were all

Figure 3.1: Representative frequency distributions of PHI data from the 1988/89 cultivar evaluation trial. Distribution A is exemplified by a high number of barren and poor performing plants with the data shown for CVN replicate 1. Other examples of this distribution were CVN replicate 2, CLN replicate 2, and SLU replicates 1 and 2. Distribution B is exemplified by a high number of barren plants, with few poor performing plants. Data is shown for CLU replicate 2, while a similar distribution was observed for CLU replicate 1. Distribution C is exemplified by low numbers of barren and poor performing plants, as shown for SVU replicate 2. Other examples of this distribution were SVU replicate 1, CVU replicate 1 and 2 at CLN replicate 1.

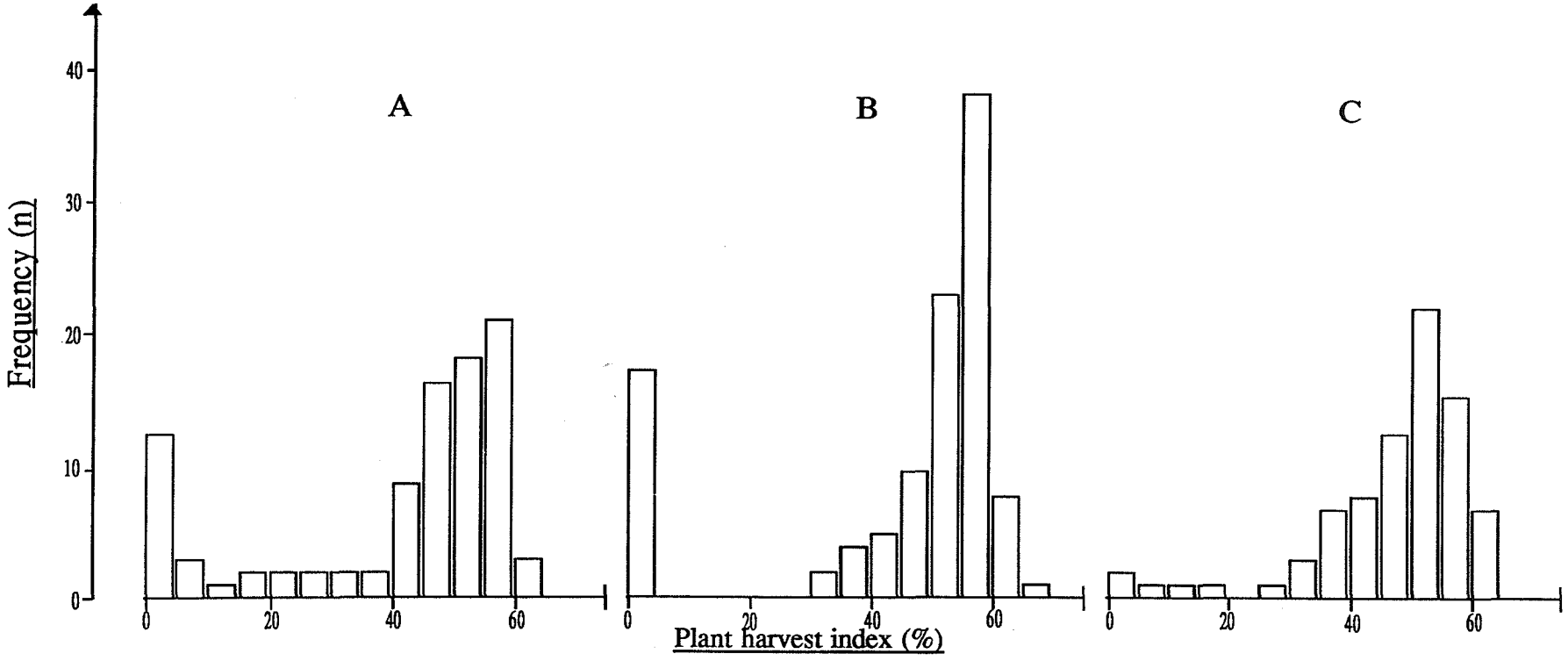


Table 3.3: Summary of plant harvest index data from the 1988/89 cultivar evaluation trial. †Explanations of the three distribution forms are given in Figure 3.1. Where significant replicate differences were found for PHI, values for both replicates are given. For the remaining genotypes, the genotype mean is presented with the SEM in parenthesis.

* Values within a column with a letter in common are not significantly different ($p<0.05$)

Genotype	†Distribution form	Plant harvest index (%)			Poor performing plants			
		Mean	Median	CV	% of total number		% of TBY	
					Barren	PHI ≤33%	Barren	PHI ≤33%
CVN	A	38.6_{cde}*	46.2	49.2	12.6_{a}	25.3_{ab}	3.5_{a}	12.0_{ab}
		(0.02)			(0.8)	(0.5)	(0.19)	(0.65)
CVU	C	44.6_{bc}	47.9	25.3	0_{b}	7.0_{d}	0_{a}	4.8_{b}
	C	38.8_{de}	40.3	23.2	(0.0)	21.0_{abc}	(0.0)	16.7_{a}
CLN	C	55.4_{a}	59.4	27.3	2.2_{b}	10.2_{c}	2.7_{a}	5.7_{b}
	A	36.5_{de}	44.1	54.5	12.9_{a}	29.0_{a}	(1.16)	15.6_{a}
CLU	B	49.6_{b}	54.9	32.8	11.8_{a}	15.3_{abcd}	3.1_{a}	5.5_{b}
	B	42.1_{cd}	51.9	49.7	(5.35)	(4.95)	(0.53)	(0.82)
SLU	A	33.1_{e}	38.6	46.2	7.7_{ab}	19.1_{abc}	3.6_{a}	11.9_{ab}
	A	42.0_{cd}	47.7	34.5	(3.04)	(6.55)	(0.50)	(1.58)
SVU	C	42.7_{c}	46.4	28.5	2.5_{b}	13.0_{bcd}	1.3_{a}	7.4_{ab}
		(0.64)			(0.25)	(1.45)	(0.27)	(0.7)

below 30 %, and in the similarity between mean and median values which differed by less than 4 % (Table 3.3). The crop from replicate 2 of genotype CVU was the anomaly within this group. It contained much higher numbers of poor performing plants than the other four crops in the group although its CV was only 23.2 % (Table 3.3).

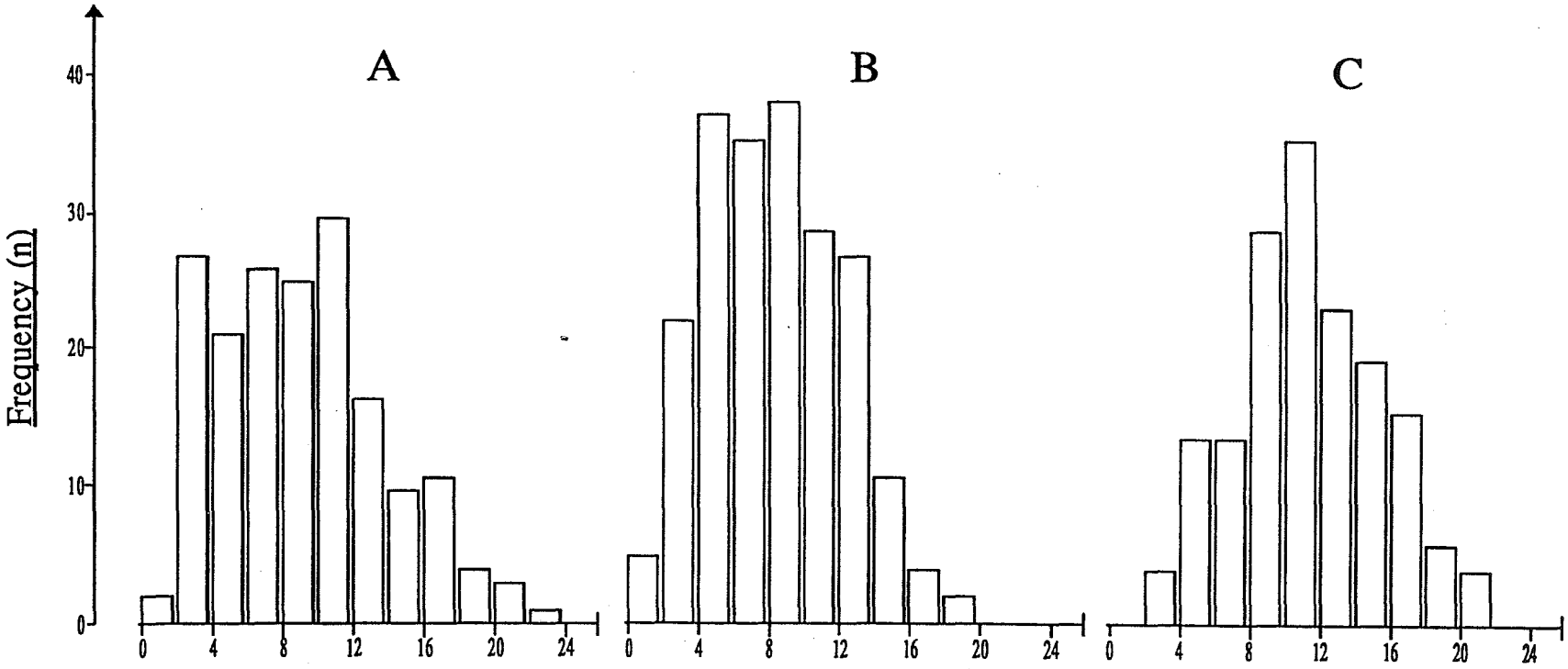
Despite the differences in the shape of the PHI distributions from these six genotypes, the maximum PHI value from all 12 crops was consistent at 60-65 %.

3.2.3 PWT Distributions

The consistency of results between replicates for the mean PWT values and the skewness, kurtosis and normality of distributions allowed PWT data to be pooled for each genotype. The mean PWT from genotype SVU (10.5 g) was significantly ($p<0.05$) higher than that from genotype CVU, which produced plants with the lowest mean PWT of 7.0 g (Figure 3.2). The median PWT values were generally lower than the mean but by less than 0.4 g.

The PWT distributions for genotypes CVN and CVU were both positively skewed ($p<0.01$) with genotype CVU also leptokurtic (Figure 3.2A). In contrast, genotypes CLU and SLU were non-normal, non-skewed and non-kurtotic (Figure 3.2B). The PWT data for CLN and SVU was considered normally distributed and had the lowest CV values (Figure 3.2C).

Figure 3.2: Representative frequency distributions for PWT data from the 1988/89 cultivar evaluation trial. Distribution A is from data for genotype CVN and was positively skewed with a CV of 57.9 %. This distribution was also representative of CVU with a CV of 43.5 %. Distribution B is from data for genotype CLU (CV=52.1 %) and represents a non-normal, non-skewed, non-kurtotic distribution. This distribution form was also found for SLU (CV=49.5 %). Distribution C is from data for SVU (CV=37.5 %) and represents a normal distribution. Data from CLN (CV=40.4 %) was also normally distributed.



3.2.4 Relationship Between SWT and PWT

The relationship between SWT and PWT was investigated using regression analysis for each crop. In all 12 cases, a strong linear relationship was found with each coefficient of determination (R^2) between 0.79 and 0.96 (Table 3.4). The relationships are illustrated in Figure 3.3 by data from the same crops used to represent the three forms of PHI distributions (Section 3.2.2). The 12 regression equations all had SWT axis intercepts below zero ($p<0.01$) with gradients between 0.52 and 0.73.

Analysis of covariance was used to compare the coefficients of the regression equations, between replicates. The results indicated a single equation could be used to describe genotypes CVN and SVU, but significantly different intercepts were found between replicates of genotypes CVU, CLU and SLU. A significant gradient difference was found between replicates for genotype CLN (Table 3.4).

Analysis of covariance results indicated that leverage was not a significant problem. The MPW values were calculated from the regression coefficients and these ranged from 0.89 to 2.66 g plant^{-1} (Table 3.4).

3.2.5 Relationship Between PHI and PWT

The barren plants and those with low PHI values generally came from plants of low PWT (Figure 3.4). However, some plants with similarly low PWTs also had PHI values of up to 50 % (Figure 3.4A-C).

Table 3.4: Summary statistics for regression analysis of SWT against PWT for data in the 1988/89 cultivar evaluation trial. Minimum plant weight values are derived from regression values (Section 3.3.2). Standard errors ranged between 0.100 and 0.277 for the intercept, and between 0.012 and 0.033 for the gradient.

	Regression Values				Coefficient of determination (%)		Minimum plant weight (g)	
	Intercept		Gradient					
Replicate	1	2	1	2	1	2	1	2
Genotype								
CVN	-0.97	-1.16	0.57	0.59	87.0	96.1	1.69	1.96
CVU	-0.48	-0.82	0.54	0.52	92.8	94.4	0.89	1.56
CLN	-1.17	-1.56	0.73	0.64	89.0	86.1	2.47	1.31
CLU	-0.64	-0.78	0.63	0.51	85.9	94.6	1.60	1.02
SLU	-1.37	-0.76	0.51	0.54	92.1	88.9	2.66	1.41
SVU	-1.19	-0.71	0.56	0.53	86.8	78.7	2.13	1.34

Figure 3.3: Relationship between seed weight and plant weight for data from field pea crops in the 1988/89 cultivar evaluation trial. Data is presented to represent each of the three PHI forms shown in Figure 3.1. Data is from CVN replicate 1 for Figure 3.3A, CLU replicate 2 for Figure 3.3B, and SVU replicate 2 for Figure 3.3C. The figures include the regression equation and coefficient of determination (R^2) in parenthesis.

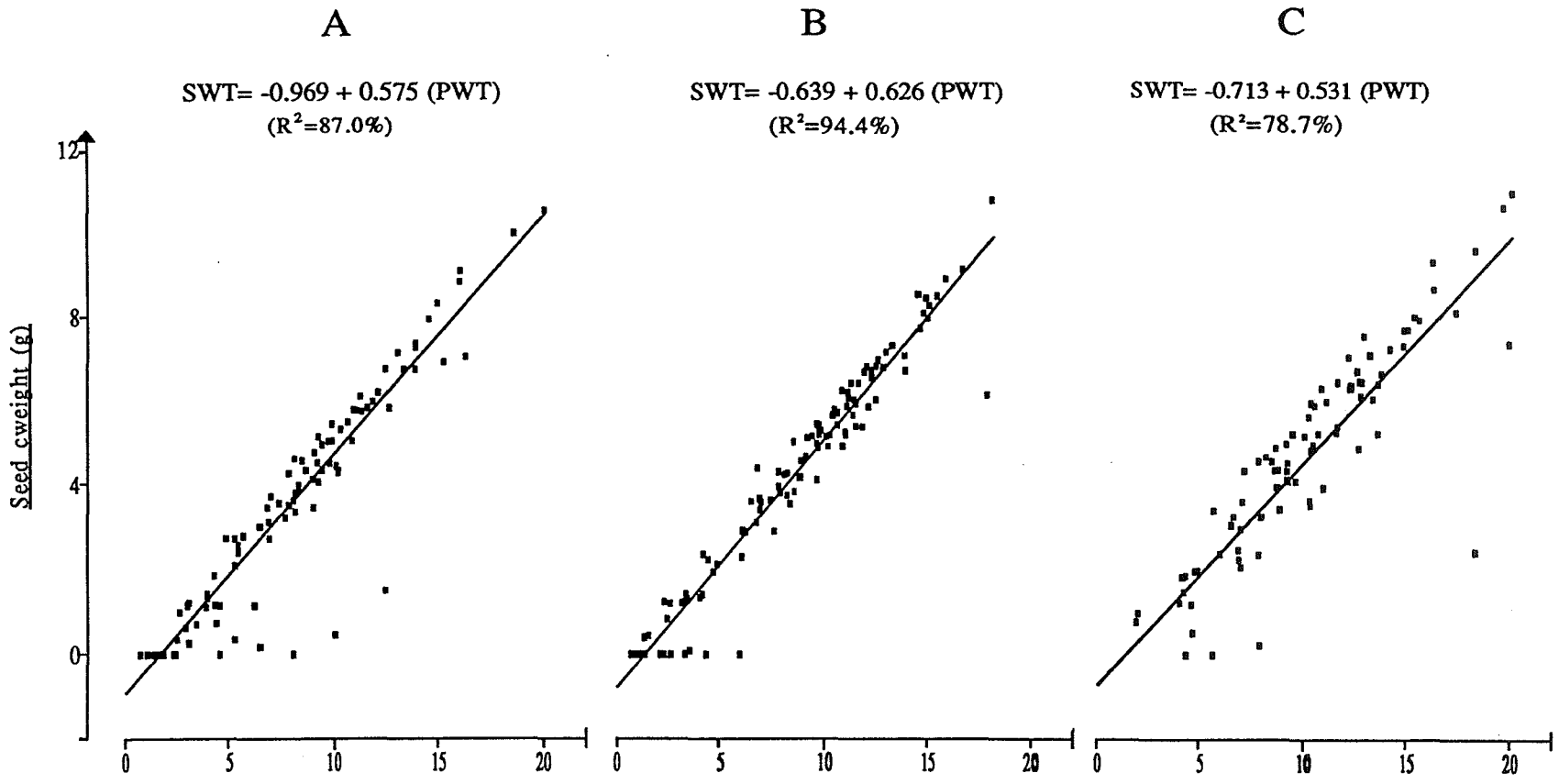
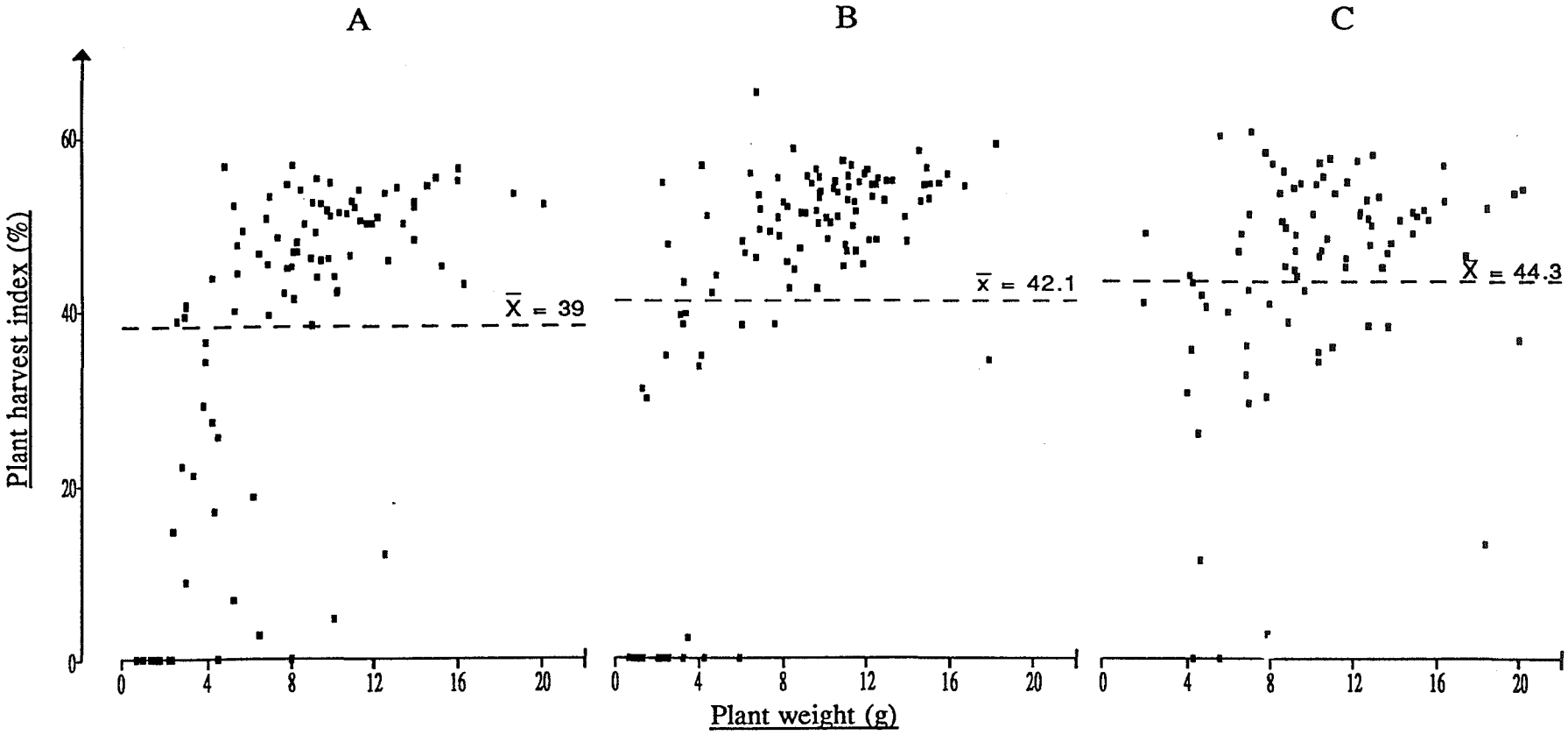


Figure 3.4: Relationship between plant harvest index (PHI) and plant weight (PWT) for data from field pea crops in the 1988/89 cultivar evaluation trial. Data is presented to represent each of three PHI distribution forms shown in Figure 3.1. Data is from CVN replicate 1 for Figure 3.4A, CLU replicate 2 for Figure 3.4B, and SVU replicate 2 for Figure 3.4C. The mean PHI values are represented by the dashed line in each Figure.



3.3 DISCUSSION

Yield results from this trial were used to screen the 60 genotypes for inclusion in future trials in the DSIR field pea breeding programme. However, the discussion for this study focuses on the selection and quantitative description of the six morphologically distinct genotypes selected from the original 60. These six genotypes were chosen from the qualitative descriptions given in Table 3.1, with no non-uniform semi-leafless genotypes found.

The aim of relating these plant types to differences in yield and CHI was not achieved, due to the variation between replicates for some genotypes, and the relatively small number of replicates (associated with the need to maximize the number of genotypes available for selection).

Replicate variation was generally significant for seed yield and PHI values with greater agreement between replicates for PWT. This implies that the reproductive growth of the plants was affected more than their vegetative growth. This finding is consistent with the application of irrigation water across the trial. That is, the availability of adequate irrigation was affected by a severe drought during the season, and this prevented optimum timing, duration and uniformity of irrigation applications across the trial area, particularly later in the season (W.A. Jermyn pers. comm.). This lack of uniformity in irrigation was probably the main cause of yield differences between the replicates of a genotype.

An important objective of the experiments described in the following chapters was therefore to minimize agronomic variability, so that the effects on yields and harvest indices of the different plant types could be isolated.

Although the causes of seed yield variability could not be attributed to morphological characteristics of each genotype, it was possible to compare these results with those from

trials reported by Ambrose and Hedley (1984) and test the assumptions that initiated this study. These were: that PHI distributions vary among genotypes, that a relationship exists between seed yield and the PHI distribution, that plants with low PHI values tend to come from plants of low PWT, and that a linear relationship exists between SWT and PWT (Ambrose and Hedley, 1984).

3.3.1 Seed Yields and PHI Distributions

The PHI values from the 12 crops in this trial were summarized as producing one of three distribution forms. These distributions offer some insight into the causes of seed yield variations. For example, both replicates from genotype SVU were classified in the third distribution form and contained few barren or poor performance plants, had low CV values (Table 3.3), and were associated with a relatively high seed yield of about 400 g m^{-2} (Table 3.2). In contrast, genotype CVN was classified in the first distribution form and contained a high proportion of both barren and poor performing plants, which resulted in a high CV of 49.2 % (Table 3.3) and a lower seed yield of about 350 g m^{-2}. Replicate 1 of genotype CLN had a similar PHI distribution (Figure 3.1C) and seed yield (Table 3.2) to that of genotype SVU. In contrast, the PHI distribution and seed yield from replicate 2 of genotype CLN were similar to those from genotype CVN (Figure 3.1A and Table 3.2) and produced a CV of 54.5 % which was double that from replicate 1 (Table 3.3). These results suggest that the distributions with fewer barren and poor performing plants, and lower CV values were associated with higher seed yields and, that the dispersion of the PHI distribution could also be related to the seed yield.

The results from genotype SLU indicate that the mean PHI is also an important component of the association between PHI distributions and seed yields. The PHI distributions from both replicates of genotype SLU were classified with genotype CVN (Figure 3.1A). However, for SLU, both replicates contained similar proportions of barren and poor performing plants (Table 3.3) but their seed yields varied (Table 3.2). The

lower seed yield for replicate 1 (310 g m^{-2}) reflected its lower mean PHI value of 33.1 % and the CV of 46.2 % (Table 3.3). In comparison, the seed yield of 421 g m^{-2} for replicate 2 was associated with a significantly higher mean PHI of 42.0 % and lower CV of 34.5 % (Table 3.3).

Over all the results from this trial support the idea of an association between seed yield and PHI distributions (Ambrose and Hedley, 1984). Furthermore, the results indicate that the relationship depends on both the dispersion or shape of the PHI distribution, as indicated by the CV or SD values, and its location (mean).

Genotypes from the third distribution type had fewer poor performing and barren plants, and subsequently lower CV values, than genotypes from the first two distribution types. Genotypes in this category were therefore closer to the hypothesized ideal situation of high PHI values for all plants in the population (Ambrose and Hedley, 1984). Both replicates of genotype SVU were in this third PHI category and these crops also had a higher seed yield than those from genotype CVN which had both replicates grouped in the first PHI distribution category. This is therefore the first indication that, when sown at 100 plants m^2, genotype SVU may possess more traits associated with uniformly high individual PHI values than genotype CVN.

However, the association between high seed yields and the third distribution type was inconsistent. Both replicates from genotype CVU also produced this favourable distribution form, but its seed yields were lower than from SVU, and were influenced by the agronomic variability. For genotypes CVU, replicate 2 produced approximately 25 % more dry matter than replicate 1 but only 5 % more seed, and consequently had a lower CHI value (Table 3.2). The lower CHI value for replicate 2 indicates that it failed to convert the same proportion of the dry matter to seed in both replicates. This reduced in conversion efficiency is consistent with the idea of moisture stress during the reproductive growth of the crop (Ritchie, 1990). In contrast, the lower biological yield for replicate 1 indicates moisture stress may have occurred during the vegetative growth phase of this

crop. Consequently, the maximum potential seed yield for replicate 1 was lower than for replicate 2, even though its CHI was higher.

The variation in shapes of the PHI distributions types was also highlighted by the deviation between mean and median values. For the third distribution type, with fewer barren and poor performing plants, the median PHI values were less than 4 % higher than the mean values. In contrast, for the first and second distribution forms, which contained greater numbers of barren and poor performing plants, the median values were between 5.2 and 9.7 % higher (Table 3.3).

Despite the distinct differences in the forms of PHI distributions, none of the crops from this trial resulted the even spread of PHI values, or the 30 to 60 % barren plants, observed for a low yielding genotype by Ambrose and Hedley (1984). Thus, the link between PHI distributions and seed yield was less defined in this trial than in that previously reported by Ambrose and Hedley (1984).

In the plant population experiment described in Chapter 5 an objective is to minimize the agronomic variation among crops and then to examine whether the resulting PHI distributions were similar, or of contrasting forms to those found in this trial, or described by Ambrose and Hedley (1984).

3.3.2 SWT, PWT and MPW

The results from this cultivar evaluation trial also supported the observation that low SWT and PHI values generally come from the smaller plants in a crop. The data in Figure 3.4 show that most of the barren or poor performing plants also had low PWT values.

Regression results indicated that, regardless of the genotype, seed yield, or form of the PHI distribution form, there was a strong linear relationship between SWT and PWT (Figure 3.3; Table 3.4). This linear relationship is consistent with results for other species (Prihar and Stewart, 1990; Gardner and Gardner, 1983) as well as for field peas (Hedley and Ambrose, 1981). The SWT axis intercept produced from each of the 12 crops was below zero (Table 3.4). These negative intercepts imply that a MPW was required before harvestable seed was produced by the field pea plants. Values of the MPW were estimated from the results in Table 3.4 by inverse prediction of the PWT for a SWT of zero (PWT axis intercept). These values ranged from 0.89 to 2.66 g plant^{-1}.

Although MPW values were indicated for each crop, the estimates of MPW were not taken as absolute threshold values for each genotype, because some of the plants which had dry weights similar to the predicted MPW values produced PHI values of over 40 % (Figure 3.4). On the other hand, some of the barren plants had PWT values of up to 8.0 g, which exceeded the calculated MPW values. Furthermore, the complication of non-uniform irrigation means these results cannot be used to determine whether the MPW was species dependent and expected from all field pea crops, or was produced due to the stress experienced by individual plants within the population (Prihar and Stewart, 1990). In Chapters 6 and 8 the idea of a MPW is discussed in greater detail, after evaluation under more uniform agronomic conditions, to determine whether a MPW is an artefact resulting from variable stress on plants within crops (Prihar and Stewart, 1990), or is an inherent characteristic of field pea crops.

The occurrence of plants in a crop with similar dry weight but different reproductive performance may result from differential interplant competition during growth. In particular, plants of similar dry weight with small or large neighbours may experience interplant competition at different times or intensities (Ford, 1975; Cannell *et al.*, 1984). To identify variations in the reproductive performance of plants, the growth of individuals within the population needs to be examined during the season, with some reference to the activity of neighbouring plants. The populations should be grown at precise spacings to

minimize the competitive pressures from non-genetic sources. An assessment of the competitive pressure on the whole crop and the localized effect of neighbours on individual plants would then be possible.

3.3.3 PWT Distributions

The PWT distributions from crops in this trial all had similar locations, as indicated by their mean and median values (Section 3.2.3), but the degree and type of dispersion varied between genotypes. For both conventional vigorous genotypes (CVN and CVU), distributions were positively skewed, whereas they were normally distributed for genotypes SVU and CLN and non-skewed, non-kurtotic and non-normal for genotypes CLU and SLU.

Frequency distributions of PWT that follow a normal distribution are usually observed during seedling emergence and early growth, when interplant competition is low (Ford, 1975). Normality may also occur after self-thinning has removed the understorey of a crop from previously positively skewed distributions (Benjamin and Hardwick, 1986). The observation of both normal and positively skewed distributions in these genotypes, supports the hypothesis that the crop community initially has a normal PWT distribution, that becomes positively skewed in proportion to the degree of interplant competition as the plants mature (Benjamin and Hardwick, 1986).

The reasons that normal PWT distributions and lower CV values were found for genotypes SVU and CLN are unclear, but they may have resulted from less interplant competition within crops from these two plant types than from within the crops from the conventional, vigorous plant types.

3.4 SUMMARY

In summary, the 1988/89 cultivar evaluation trial was used to select six morphologically distinct genotypes from a pool of 60. Selections were based on leaf type, growth vigour, and the degree of uniformity within the plant populations when seedlings were 45 days old. These contrasting plant types are used in the experiment and analyses described in the following chapters, to examine the relationship between seed yield and the morphological characteristics of these genotypes.

Large differences in results between replicates made it impossible to distinguish between these six genotypes on the basis of differences in their yields or CHI values. However, it was possible to distinguish between these genotypes using plant distribution parameters. It was also possible to draw several important general inferences about dried pea crops from the results of this trial. These included indications that:

1) differences in both location (mean) and dispersion (SD) of PHI distributions were associated with seed yield differences (Section 3.3.1),
2) barren and poor performing plants tended to be the smallest plants in a population (Section 3.3.2),
3) maximum PHI values were similar for all genotypes with values at 60-65 % (Figure 3.1),
4) there was a strong linear relationship between SWT and PWT values, regardless of the genotype or its seed yield (Section 3.3.2; Figure 3.3),
5) there was a negative SWT axis intercept for the linear relationships between SWT and PWT, and thus MPW values were calculated (Section 3.3.2),
6) there were both normal and positively skewed frequency distributions for PWT (Section 3.3.3).
7) to isolate the influence of plant type on PHI values and seed yield, agronomic variability must be minimized, with some emphasis on the effects of neighbours required.

These results agree in principle with the hypotheses proposed by Ambrose and Hedley (1984), and therefore satisfied the main objective of this initial trial.

To utilize the associations between PHI, SWT and PWT found in this trial, and therefore to develop an approach for the description of crop yields based on the individual plant characteristic distributions, a more formal analytical framework is required. In Chapter 4, an empirical statistical model based on the distributions of individual plant characteristic is developed. This model is based on the results from this chapter and previous observations made by Ambrose and Hedley (1984). Theoretical predictions of the model are then presented in preparation for model development and testing with field data in Chapters 6 and 7.

CHAPTER 4

ANALYSIS OF YIELD USING FREQUENCY DISTRIBUTIONS FOR INDIVIDUAL GROWTH PARAMETERS

4.1 INTRODUCTION

In this chapter an empirical model is proposed for analysing the yield determinants of dried pea crops. This model was developed from the observation that differences in seed yields between crops could be associated with differences in the frequency distributions for their PHI values and PWT (Ambrose and Hedley, 1984; Chapter 3). The underlying assumption from this association is that seed yield of a crop is dependent on the behaviour of individual plants within the crop.

In Section 4.2 the biological and statistical basis for the model and its components are outlined. The development of the model is then based on a series of simulations which examine the theoretical effects of differences in the frequency distribution (FD) values (mean and SD) of SWT and PWT on the components of the model (Section 4.3). In Section 4.4 boundary conditions are defined for the model and their implications are investigated through further simulations. The consequences for PHI of changes in the components of the model are discussed in Section 4.5. A comparison of different statistical techniques is presented in Section 4.6 and the major findings of the chapter are summarized in Section 4.7.

4.2 BASIS OF THE MODEL

The proposed model is based on the finding of Ambrose and Hedley (1984) that seed yield differences among field pea crops are associated with different patterns of PHI distributions from the population of plants within each crop. Since PHI values are derived from SWT and PWT values:

$$PHI = (SWT/PWT) \times 100 \qquad \text{(Equation 4.1),}$$

the hypothesis from these observations is that differences in the relationship between the SWT and PWT of individual plants are the primary cause of seed yield differences among crops.

Specifically, the sum of the PWT values gives the biological yield for the crop and the seed yield then depends on the CHI, which reflects the relationship between the SWT and PWT of the individual plants (i) in the crop:

$$CHI = \Sigma_1^n [SWT_i/(\Sigma_1^n PWT_i)] \qquad \text{(Equation 4.2).}$$

Determining the relationships among FD values of SWT, PWT and PHI distributions of pea populations are therefore proposed as a method to explain seed yield differences between crops. Describing the manner in which these FD values differ among populations is the key to understanding how they are associated with seed yields. The relationship between SWT and PWT distributions therefore forms the basis of the model developed in this chapter.

4.2.1 Principal Axis Analyses

Analyses based on the principal axis technique described by Sokal and Rohlf (1981) were used to investigate the relationship between SWT and PWT. This technique

measures and characterises the intensity of association between two normally distributed variables in a bivariate scattergram. When both variables have the same unit of measure (dry weight in grams for this model) the principal axis is the first component defining the relationship between them. The second component of the model is an ellipse, which is symmetrical about this principal axis and encloses a predetermined proportion of the observations.

The relationship between SWT and PWT is therefore described by two quantifiable components, the line and the ellipse. These have been combined together in this study and defined as the principal axis model (PAM).

The aim in this chapter is to show that all dried pea crops can be described by this PAM, and that differences in the FD values of SWT and PWT of crops can be represented by differences in;

1) the intercept or gradient of the principal axis,
2) the location or shape of the ellipse, or
3) a combination of 1 and 2.

Initially, changes in the FD values of SWT and PWT are considered for bivariate normal distributions with the emphasis on how changes affect the principal axis and ellipse.

4.3 MODEL DEVELOPMENT

An empirical approach was used to determine the effects of changes in FD values. It consisted of creating a data set to mimic a crop (defined as the control) and then perturbing FD values and analysing the consequences in terms of changes in the principal axis and ellipse of the model. The initial data set was based on data in Chapter 3 which had a mean PWT of around 10 g for field pea crops sown at a commercial population of 100 plants m^{-2}.

4.3.1 Definition of the Control Crop

4.3.1.1 Calculation of the principal axis. The control position for the line and ellipse were defined by generating 100 random numbers from a normal distribution with a mean of 10 and SD of 1 using the *'MINITAB'* statistical package (Minitab, 1989). The SD of 1 was arbitrarily chosen to represent a crop with little innate variation and therefore a CV of 10 %, which is considered low for field peas. The SWT data associated with these PWT values were calculated using a linear equation to represent the relationship between SWT and PWT:

$$SWT_i = -0.5 + 0.6 \times PWT_i + E_{ij}, \qquad \text{(Equation 4.3)},$$

where E_{ij} was an error term generated randomly to give this relationship a correlation coefficient of 0.91, which was similar to those found in the cultivar evaluation trial. The coefficients for Equation 4.3 were also chosen as representative of the previous SWT versus PWT relationship (Chapter 3). From these parameters a population was simulated for the control crop which produced a mean SWT of 5.5 g with a SD of 0.61 g, and a mean PWT of 10.0 g with a SD of 0.95 g. This control population was described using methods outlined by Sokal and Rohlf (1981) to calculate an ellipse containing a predetermined percentage of the observations, 100(1-α)%, and also the principal and minor axes of the ellipse. For simulations in this chapter α was set arbitrarily at 0.25, so 75 % of the observations were expected to be contained within each ellipse. The value of F at α=0.25 with 2 and 98 degrees of freedom ($F_{\alpha[2,n-2]}$) was 1.40 for all of the simulations involving 100 data points in this chapter. Equally, any other value of α could have been selected to define an ellipse containing a different percentage of the data points.

For the control crop the equation of the principal axis was calculated to be;

$$SWT = -0.77 + 0.62 \times PWT \qquad \text{(Equation 4.4)}.$$

The SWT axis intercept, the PWT coefficient and the SD for PWT in this simulated control crop differed from the defined values because of the inclusion of the error term in Equation 4.3, and the consequent variability of the 100 random numbers generated.

4.3.1.2 Calculation of the ellipse. To construct an ellipse containing 75 % of the data points, the mean, SD, and covariance of the two populations are required. The shape of the ellipse is determined by quantifying variability along the principal axis and the minor axis which runs perpendicular to it (Figure 4.1). This variability is defined by calculating the eigen values of the variance-covariance matrix of SWT and PWT. The eigen value representing variance along the principal axis (λ_1) is;

$$\lambda_1 = \tfrac{1}{2}[SWT_v + PWT_v + \sqrt{(SWT_v+PWT_v)^2 - 4(SWT_v*PWT_v-COV)}] \quad \text{(Equation 4.5)}$$

where SWT_v is the SWT variance, PWT_v is the PWT variance and COV is the covariance between SWT and PWT.

The eigen value (λ_2) for the minor axis is;

$$\lambda_2 = SWT_v + PWT_v - \lambda_1 \quad \text{(Equation 4.6)}$$

An indication of the shape of the ellipse is gained from the axes ratio:

$$\text{Axes Ratio} = \sqrt{\lambda_1 / \lambda_2} \quad \text{(Equation 4.7)}$$

For data sets with a high correlation between SWT and PWT, the individual points are located close to the principal axis, until all points lie on the line when the correlation coefficient (R) equals one. Conversely, as R tends towards zero the points will be dispersed over an increasingly large area, and the lengths of the principal and minor axes will tend to become equal with their ratio approaching one. This technique is analogous

to principal components analyses in two dimensions with the eigen values used to represent the variance along each axis (Sokal and Rohlf, 1981).

Throughout the first 16 simulations the correlation coefficient was maintained at 0.91 to ensure that the effects of changes in the FD values could be isolated (Section 4.3.2). Consequently, simulations with high axes ratios had points spread along the principal axis more than simulations with low axes ratio values.

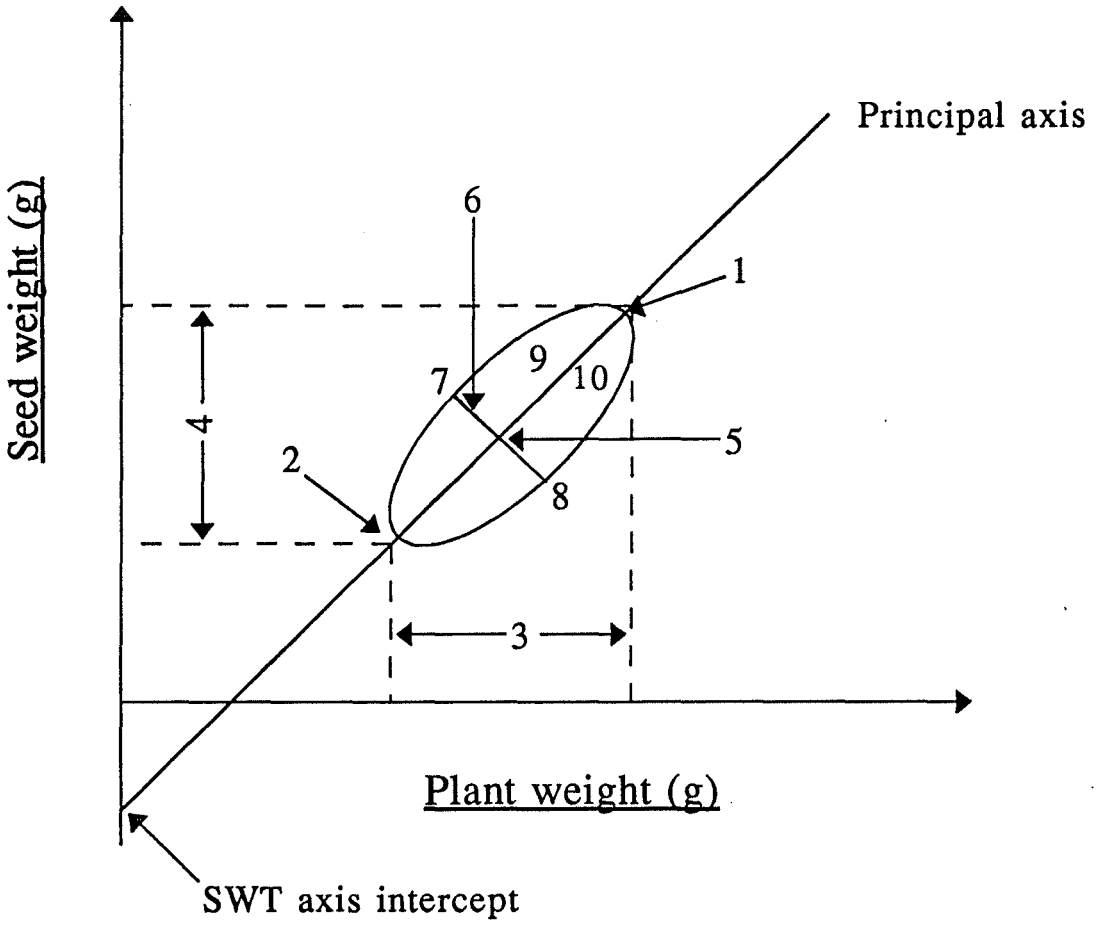
The outline of the ellipse, including the intersection points for the ellipse and the minor axis were calculated using the techniques described by Sokal and Rohlf (1981). The lower apex (LA) and upper apex values (UA) were defined as the lower and upper intersection points of the principal axis and the ellipse respectively (Figure 4.1). The projected lengths (PL) of the ellipse on both the PWT and SWT axes were also calculated:

$$PL_i = UA_i - LA_i \qquad \text{(Equation 4.8)},$$

where i = either PWT or SWT and UA and LA are the relevant upper and lower coordinates (Figure 4.1). A change in the projected length on either axis gives an indication of changes in the SD of the SWT and, or PWT populations (Section 4.3.2.2).

The internal area of the ellipse is the sum of the areas of the upper and lower regions, which are above and below the principal axis respectively (Figure 4.1). For bivariate normal distributions the ellipse is symmetrical about this principal axis. The axes ratio, projected lengths and internal area of the ellipse are used in the following sections to describe the effects of simulated changes in FD values on the shape of the ellipse. The mean coordinate of the ellipse ($\overline{PWT}$, $\overline{SWT}$) allows changes in location of the ellipse to be described.

Figure 4.1: Diagram to define the terms used in the development of the PAM.



1 - Upper apex
2 - Lower apex
3 - Projected length on PWT axis
4 - Projected length on SWT axis
5 - Mean coordinate
6 - Minor axis
7 & 8 Minor axis and ellipse intercepts
9 - Upper region of the ellipse
10 - Lower region of the ellipse

4.3.2 Simulations to Test the Model

The PAM was tested by systematically altering the data set to simulate changes in the FD values of SWT and PWT. A base number was specified for the 100 randomly generated numbers to ensure that the numbers generated were consistent between simulations and therefore that the effects of changes in the FD values on the components of the PAM could be isolated. The purpose of these simulations was to demonstrate that all possible changes in the mean and SD of SWT and PWT distributions could be accounted for within the framework of the model.

Sixteen simulations were required initially to investigate the effects of either holding constant or changing each of the four FD values (mean SWT and PWT; SD of SWT and PWT). The 16 simulations were classified into four groups according to changes in the SD values. Changes in mean SWT and PWT were then simulated within each group:

1) SD held constant for PWT and SWT;
2) SD increased in equal proportions for PWT and SWT;
3) SD of SWT increases with SD of PWT held constant; and
4) SD of PWT increased with SD of SWT held constant.

The four mean SWT and PWT coordinates were determined by setting the mean PWT at 10.0 and 30.0 g and calculating the expected SWT from Equation 4.3. The 30 g PWT value was included to determine the effect of increased PWT values on the components of the PAM. Equally, any other PWT value could have been chosen with similar results expected. Defining the PWT values resulted in four mean coordinates of (10.0, 5.5), (30.0, 5.5), (10.0, 17.5) and, (30.0, 17.5) within each of the four simulation groups. Effectively, the increase from 10 to 30 g for PWT was achieved by adding 20 to each of the 100 PWT points in the simulation and 12 to the SWT points.

The result of each of the 16 simulations is illustrated graphically in Figure 4.2A-P. The corresponding values used in and produced from the simulations are presented in Table 4.1 rows A-P.

To this stage, no biological limitations of the simulations have been considered. However, some of the theoretical results are impossible to attain biologically. For example, the third mean coordinate in each group (10.0, 17.5), with SWT greater than PWT, is unrealistic in practice, but is included to balance the statistical analyses. These unrealistic situations will be considered further and dealt with after definition of the boundary conditions for the PAM in Section 4.4.

4.3.2.1 Group 1 simulations. The first simulation represented the control position (Figure 4.2A; Table 4.1A), with FD values set at those described previously (Section 4.3.1.1) with a mean coordinate of (10.0, 5.5). Simulation B examined the effect of increasing the mean PWT to 30.0 g with the other three FD values held constant (Figure 4.2B, Table 4.1B). The resulting principal axis had the same slope (0.62) but a lower SWT intercept (-13.20). The axes ratio (5.08) and projected lengths on both axes remained the same as the control.

The effect of an increase in only the mean PWT of a crop can therefore be fully described as a shift in location of the ellipse, defined by the change in the mean coordinate which moved from (10.0, 5.5) to (30.0, 5.5) in this situation. The increased mean PWT therefore produced a shift, to a parallel principal axis with a lower SWT axis intercept (Figure 4.2B).

The effect of a decrease in only the mean PWT can be inferred by considering simulation B as the control crop and simulation A as the comparison crop. The reverse effect occurs, with a shift back to the principal axis of simulation A which had the higher SWT axis intercept and a mean coordinate of (10.0, 5.5). In the remaining simulations only the

effects of increases in the FD values on the principal axis and ellipse are considered. The opposite effect is assumed for decreases. Thus, eliminating the decrease in FD values gave the 16 (2x2x2x2) possible scenarios for the comparison crops with each of the four FD values either held constant or increased (Figure 4.2; Table 4.1).

The effects of increasing only the mean SWT, to 17.5 g, were considered in simulation C. The value of 17.5 g was calculated as the expected SWT for a PWT of 30.0 g from Equation 4.3. This simulation resulted in an ellipse with the same axes ratio, projected lengths and gradient as simulation A but its location was directly above the control, as indicated by the mean coordinate (10.0, 17.5). Consequently the SWT axis intercept for simulation C had increased to 11.23 g (Figure 4.2C; Table 4.1C).

When mean values for SWT and PWT were both increased, to 17.5 g and 30.0 g respectively, the descriptors for the ellipse were the same as in simulations A to C, and the principal axis had the same gradient of 0.62, and a similar intercept, to simulation A (Figure 4.1D; Table 4.1D). Effectively, the change in mean coordinate (30.0,17.5), which defined the location of the ellipse, was the only descriptor of either model component to change. If the calculated gradients for this group of simulations (A-D) had been 0.6 as defined (Equation 4.3), then the SWT axis intercepts for simulations A and D would have been the same. Also the shift from the centre of ellipse A to the centre of ellipse D would have been along a common principal axis.

The results from simulations A to D indicate that the effects of the four changes in mean values of SWT and PWT were described in terms of changes in the principal axis and ellipse of the PAM. Namely, these changes in mean values were described by changes in the SWT axis intercept of the principal axis and the location of the ellipse. The changes in mean values did not however, alter either the gradient of the principal axis or the size and shape of the ellipse.

Table 4.1: Relationship between the simulated data sets and their derived principal axis and ellipse values. Values were used in, and calculated from, the 16 simulations (A-P) required for the development of the principal axis model as outlined in Section 4.3. The mean PWT and SWT are given as $\overline{PWT}$ and $\overline{SWT}$. PWT_{sd} and SWT_{sd} represent the PWT and SWT standard deviation values. R is the correlation coefficient for the simulation.

Simulation group	Frequency distribution values (g)				Principal axis values			Ellipse values		
								Projected lengths (g)		Axes
ONE	$\overline{PWT}$	$\overline{SWT}$	PWT_{sd}	SWT_{sd}	Intercept (g)	Gradient	(R)	PWT	SWT	ratio
A	10	5.5	0.95	0.61	-0.77	0.62	0.91	3.17	2.03	5.08
B	30	5.5	0.95	0.61	-13.20	0.62	0.91	3.17	2.03	5.08
C	10	17.5	0.95	0.61	11.23	0.62	0.91	3.17	2.03	5.08
D	30	17.5	0.95	0.61	-1.20	0.62	0.91	3.17	2.03	5.08
TWO										
E	10	5.5	1.91	1.26	-0.93	0.63	0.91	6.39	4.05	5.08
F	30	5.5	1.91	1.26	-13.60	0.63	0.91	6.39	4.05	5.08
G	10	17.5	1.91	1.26	11.06	0.63	0.91	6.39	4.05	5.08
H	30	17.5	1.91	1.26	-1.62	0.63	0.91	6.39	4.05	5.08
THREE										
I	10	5.5	0.95	1.26	-8.13	1.36	0.91	3.08	4.20	4.86
J	30	5.5	0.95	1.26	-35.4	1.36	0.91	3.08	4.20	4.86
K	10	17.5	0.95	1.26	3.87	1.36	0.91	3.08	4.20	4.86
L	30	17.5	0.95	1.26	-23.4	1.36	0.91	3.08	4.20	4.86
FOUR										
M	10	5.5	1.91	0.61	2.59	0.30	0.91	6.43	1.92	8.14
N	30	5.5	1.91	0.61	-3.37	0.30	0.91	6.43	1.92	8.14
O	10	17.5	1.91	0.61	14.59	0.30	0.91	6.43	1.92	8.14
P	30	17.5	1.91	0.61	8.63	0.30	0.91	6.43	1.92	8.14

Figure 4.2: Principal axis and ellipse locations resulting from the FD values used in the initial 16 simulations, for the development of the PAM. The data set used to create these simulations, and resulting ellipse and principal axis values are summarised in Table 4.1 (Simulation group one: A-D).

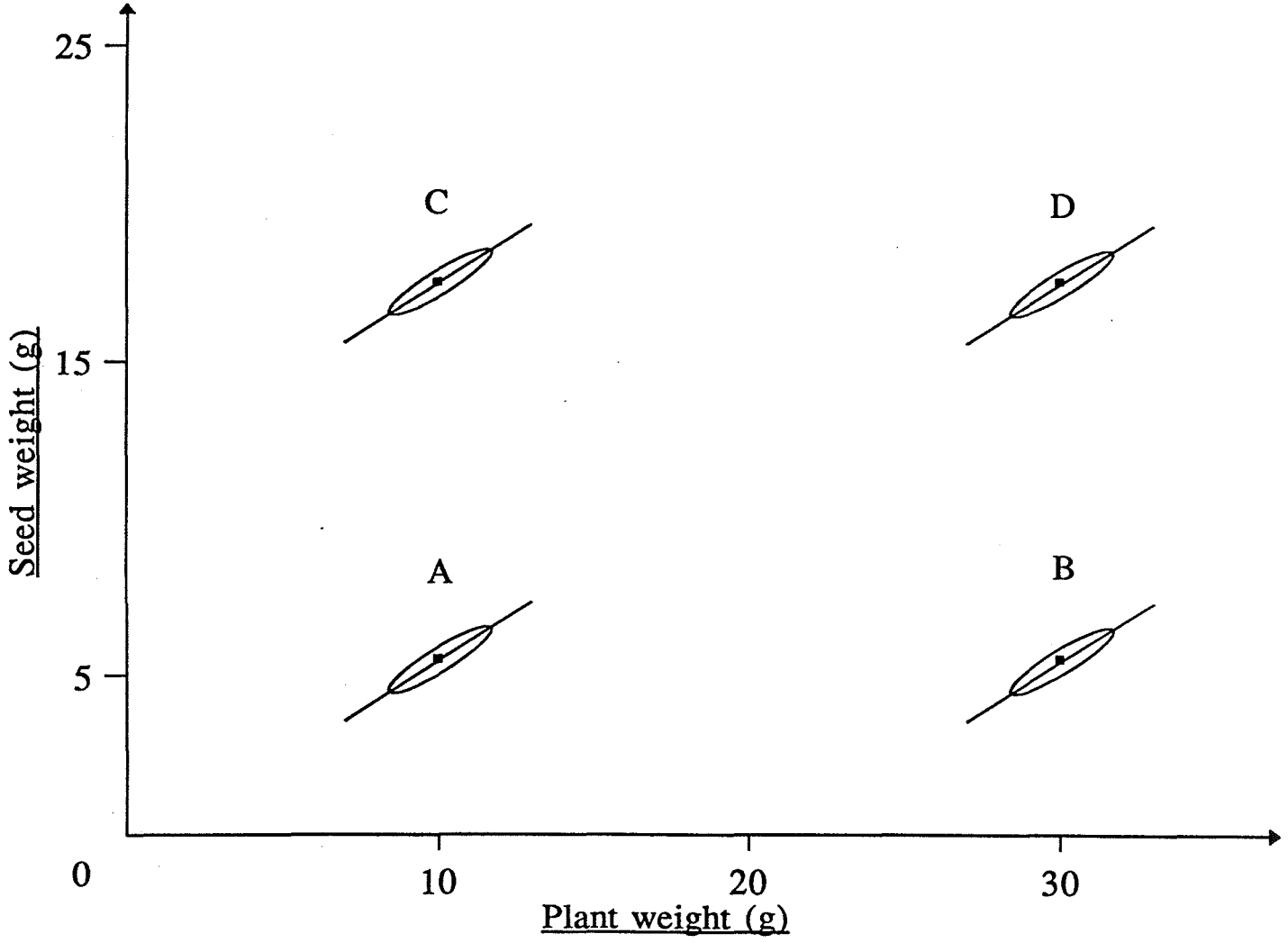


Figure 4.2: Principal axis and ellipse locations resulting from the FD values used in the initial 16 simulations, for the development of the PAM. The data set used to create these simulations, and resulting ellipse and principal axis values are summarised in Table 4.1 (Simulation group two: E-H).

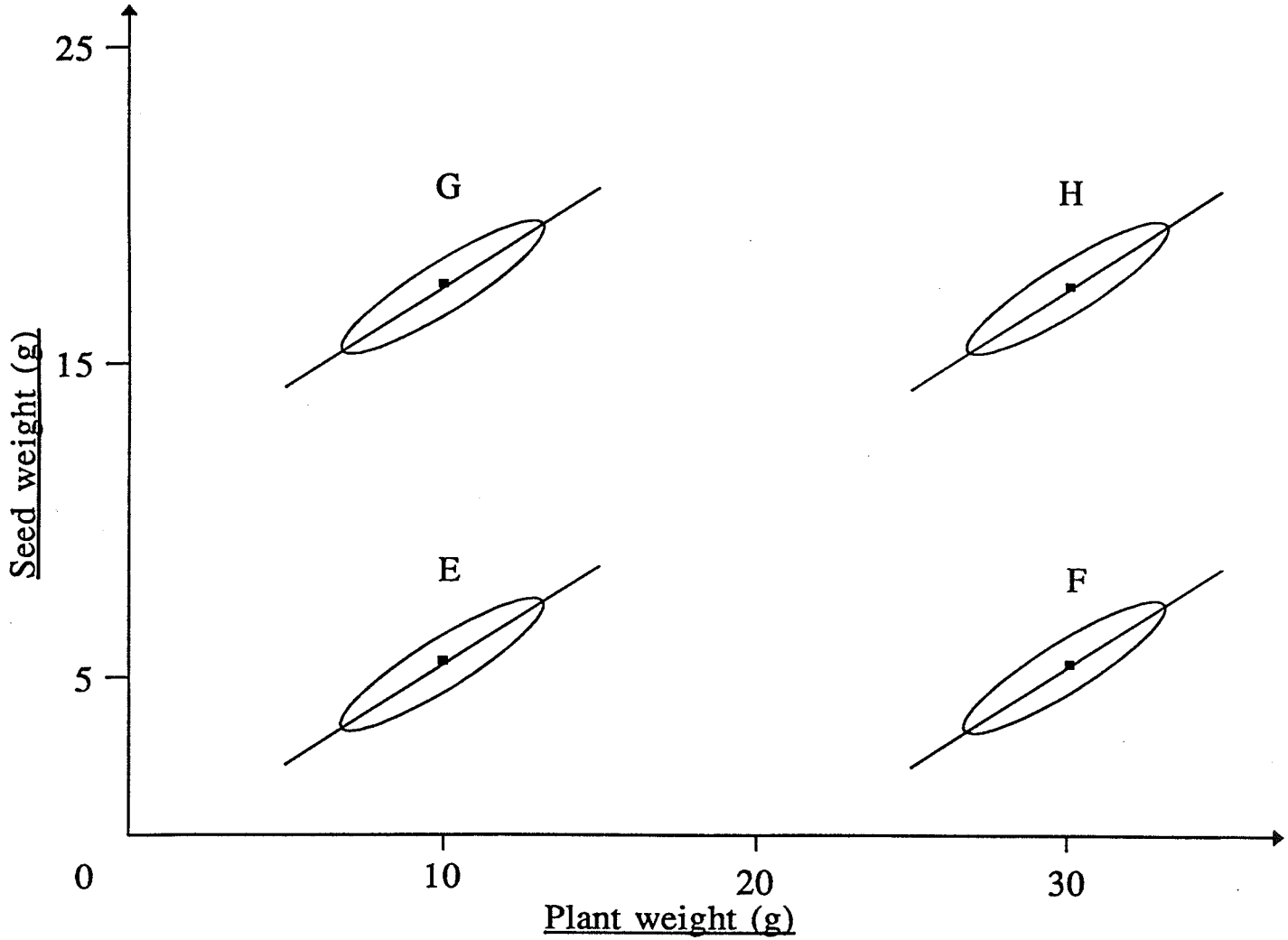


Figure 4.2: Principal axis and ellipse locations resulting from the FD values used in the initial 16 simulations, for the development of the PAM. The data set used to create these simulations, and resulting ellipse and principal axis values are summarised in Table 4.1 (Simulation group three: I-L).

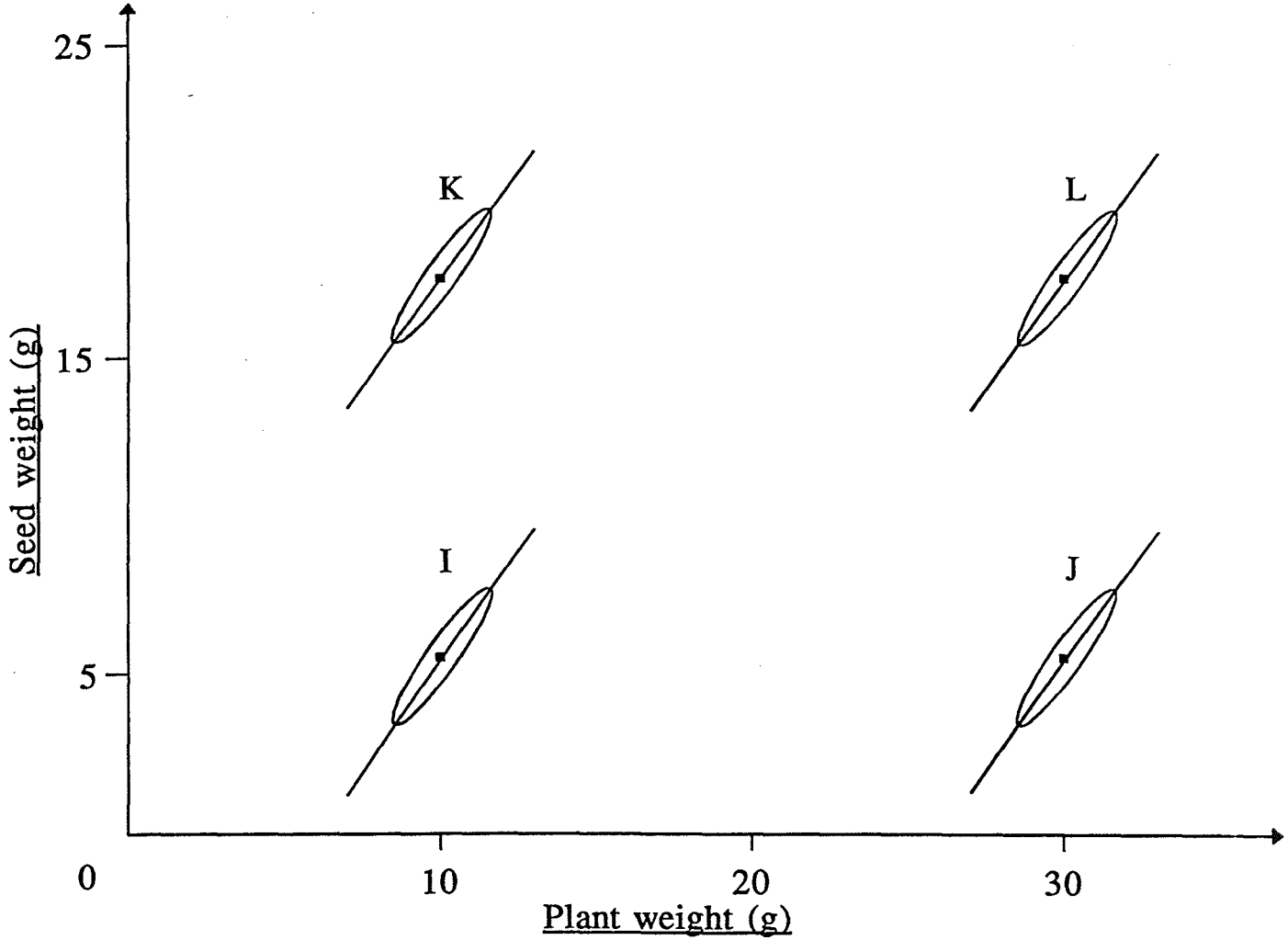
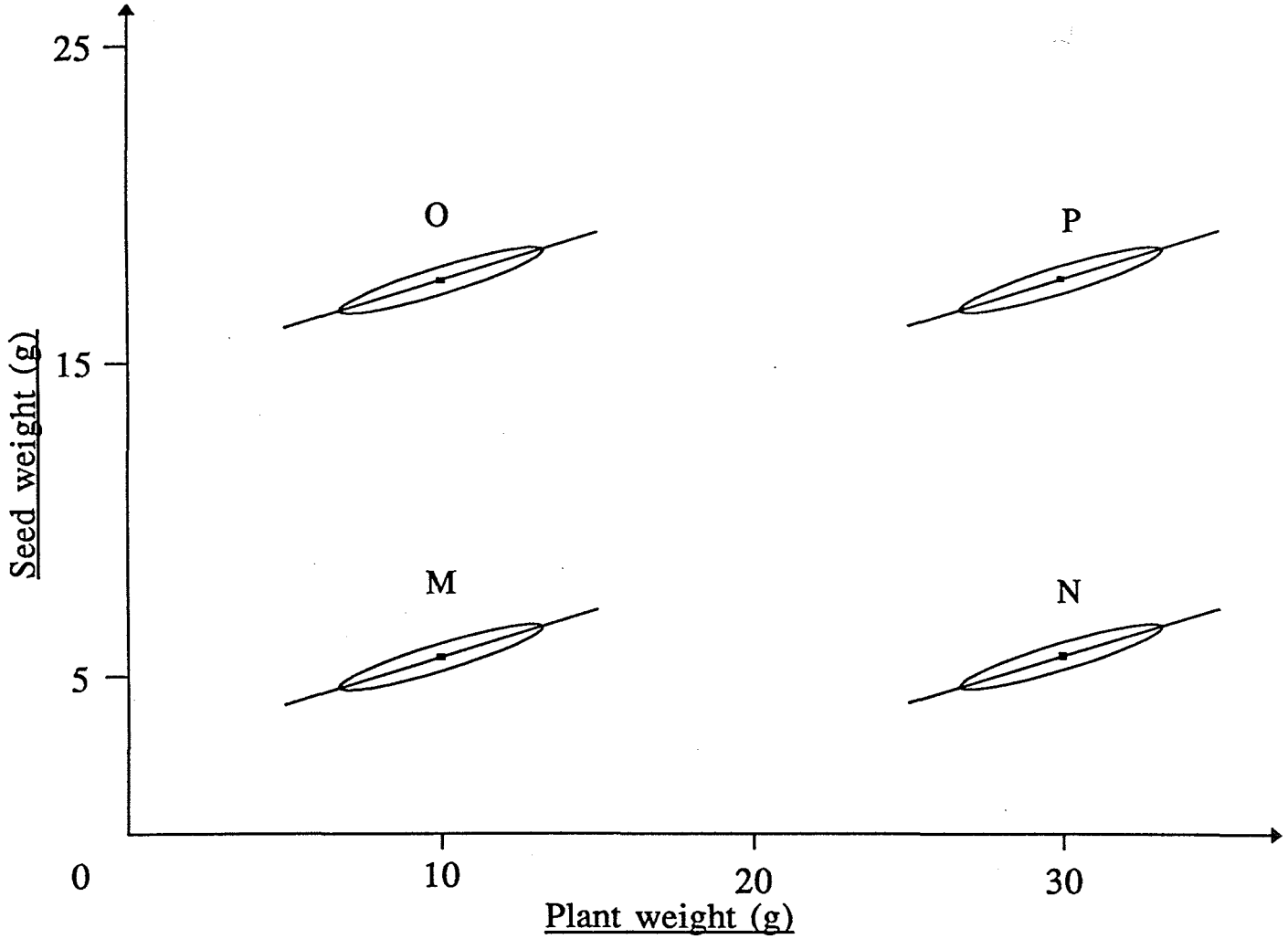


Figure 4.2: Principal axis and ellipse locations resulting from the FD values used in the initial 16 simulations, for the development of the PAM. The data set used to create these simulations, and resulting ellipse and principal axis values are summarised in Table 4.1 (Simulation group four: M-P).



4.3.2.2 Group 2 simulations. In the second group of simulations, the SD value for PWT and SWT were both approximately doubled to 1.91 g and 1.26 g. The increase in SD for PWT was achieved by generating the random numbers from a normal distribution with a mean of 10 but with the SD value increased to 2. This SD value could have been increased by any amount, with similar changes in the components of the PAM expected. The increase in SD for SWT was achieved by increasing the E_{ij} term in Equation 4.3. These higher SD values resulted in projected lengths of 6.39 g and 4.05 g on the PWT and SWT axes respectively for these group 2 simulations, compared to 3.17 g and 2.03 g for those from group 1 (Table 4.1). However, despite the changes in the projected lengths the axes ratio remained at 5.08. This consistent axes ratio suggests that the variance on both the major and minor axes was the same as that found for group 1. In addition, the position of the principal axis for simulation F was analogous to A, F to B, G to C and H to D. For example, the SWT axis intercepts for simulations E and A were -0.77 and -0.93 with gradients of 0.63 and 0.62 respectively (Table 4.1 E-H; Figure 4.2 E-H). The changes in mean coordinates were the same in both groups which also meant the locations of each ellipse were identical.

The consistency of principal axes values between these two groups of simulations, indicates that the major influence of the increased SD values was the increased internal area of the ellipse. Effectively the influence of the increased SD values has been described by an increase in the internal areas and projected lengths of the ellipses. The changes in the SWT axis intercepts and ellipse locations for group 2 simulations were again controlled by the changes in the mean coordinates (Table 4.1).

4.3.2.3 Group 3 simulations. The simulations in groups 3 and 4 investigated the effects of changes in only one of the SD values. For continuity, the SD values chosen were the same as those used in groups 1 and 2. The group 3 simulations were used to identify the effect of an increase in the SD for SWT to 1.26 g, with the SD for PWT held constant at 0.95 g.

The major effect of this change was an anti-clockwise rotation of the principal axis, with the gradient for simulations I to L increasing to 1.36 (Table 4.1I-L). The ellipse locations were again controlled by the mean coordinates but the values for the SWT axis intercepts were always considerably lower than the comparable group 1 simulations (Table 4.1I-L). For example, the SWT axis intercept for simulation I was -8.13 (Table 4.1I) compared to -0.77 for simulation A (Table 4.1A).

The projected length on the SWT axis increased from 2.03 g in group 1 simulations to 4.2 g in this group, which reflects the increased SD for SWT. The projected lengths of PWT axis were similar to those in group 1 (Table 4.1I-L).

This third group of simulations were collectively interpreted to suggest that whenever the increase in SD of SWT was greater than the increase of PWT, anti-clockwise rotation of the principal axis would occur. For example, if the SWT SD was three times that of the control, but the PWT SD only double, the resulting principal axis would appear to have rotated anti-clockwise and would have a lower intercept and higher gradient than the control.

4.3.2.4 Group 4 simulations. For the simulations in group 4 the SD for PWT was doubled to 1.91 g and the SD for SWT was held at 0.61 g. From these simulations the principal axis rotated clockwise with a decrease in the slope from 0.62 to 0.30 and the SWT axis intercepts increased. In contrast to the group 3 simulations, the projected length on the SWT axis (1.92 g) was similar to that from the control (2.03 g), but the projected length on the PWT axis approximately doubled from 3.17 g to 6.43 g (Table 4.1M-P). These changes in projected lengths indicated an elongation of the ellipse along the principal axis (Figure 4.2M-P).

This fourth group of simulations were collectively interpreted to indicate that when the increase in SD of PWT exceeds that of SWT, the principal axis will rotate clockwise and

consequently the SWT axis intercept will increase. This interpretation is the opposite to that found from group 3 simulations. That is, if the SD for SWT was double that of the control, but the SD for PWT was treble it, then the principal axis would appear to have rotated clockwise with a higher SWT intercept and lower gradient.

4.3.2.5 Summary of simulations. The principal axis model has been used to describe the effects of systematic changes in the FD values of SWT and PWT, in terms of changes in a principal axis and ellipse. The model was tested using 16 simulations which were classified into four groups. Within these groups the effects of changes in mean SWT and PWT values were examined.

Group 1) SWT and PWT SD constant (Simulations A-D)

- the slope of the principal axis and internal area of the ellipse remain constant,
- the SWT axis intercept and the location of the ellipse are dependent on the mean coordinate.

Group 2) SWT and PWT SD double (Simulations E-H)

- the principal axis retains the same gradient and SWT axis intercepts as the corresponding group 1 simulation,
- the projected lengths of the ellipse doubles on both axes and the internal area of the ellipse increases although the same axes ratio is retained.

Group 3) SWT SD increases with PWT SD constant (Simulations I-L)

- the principal axis rotates anti-clockwise about the mean coordinate, with increasing slope but decreasing SWT axis intercept,
- the axes ratio decreases due to an increase in the relative length of the minor axis,

Group 4) SWT SD constant but PWT SD increase (Simulations M-P)

- the principal axis rotates clockwise about the mean coordinate, with decreasing slope but increasing SWT axis intercept,
- the ellipse elongates along the principal axis with an increased axes ratio.

Effectively, simulation A was defined as a control crop and the other 15 simulations represented crops where at least one of the FD values differed from the control. The PAM was used to describe how the changes in FD values of these comparison crops would manifest in terms of the principal axis and ellipse.

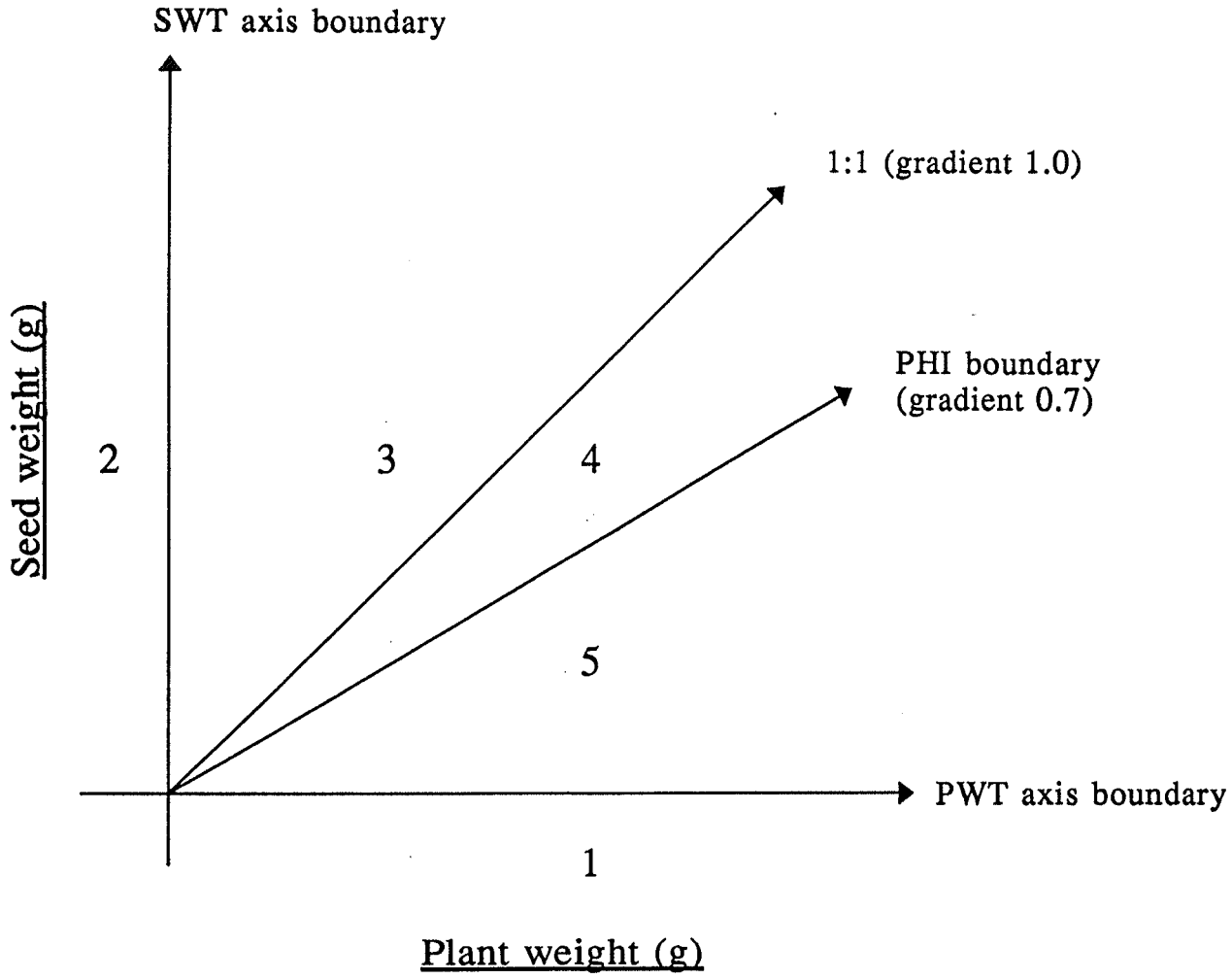
4.4 BOUNDARY CONDITIONS OF THE MODEL

These initial 16 simulations showed that the principal axis model can be used to describe systematic changes in FD values of SWT and PWT distributions. There are however, several definable limits to the PAM which are required for the descriptions of SWT and PWT values from real populations of field pea plants. These boundary conditions define more concisely the ability of the model to describe the performance of field pea crops.

4.4.1 Biological Limits

Clearly, in plant populations neither the PWT or SWT values can be negative. Graphically, this means that no part of the population can lie below the PWT axis, or to the left of the SWT axis. These axes are therefore defined as the SWT and PWT boundaries respectively (Figure 4.3). In addition, no SWT value can exceed its PWT value. A further PHI boundary therefore exists, which runs positively at a 45^0 angle from the origin, and represents the 1:1 line of SWT to PWT with a slope of 1.0. This PHI

Figure 4.3: Boundary lines for the PAM used for the analyses of dried pea crops.



Boundary regions

1 PWT values below zero

2 SWT values below zero

3 Values for SWT greater than PWT

4 Biological limit of PHI at about 70 %

5 Operating region for the PAM

boundary immediately excludes the third simulation in each of the four groups where the mean coordinate was (10.0, 17.5). The gradient of this boundary may actually be closer to 0.7 which is about the maximum harvest index attainable (Ambrose and Hedley, 1984) for an individual dried pea plant (Figure 4.3). This PHI boundary always lies inside or on the SWT boundary and subsequently the SWT boundary is redundant.

4.4.2 Implications of Biological Limits

By definition the biological limits constitute the statistical descriptions of regions where plants can not grow. In order to represent the population of plants, the components of the PAM must be constrained to prevent these boundaries from being crossed. This idea can be illustrated using the principal axes describing crops in groups 3 and 4.

Extrapolation of the principal axis from any simulations in these groups results in an intersection with the PHI boundary either above or below the ellipse (Figure 4.4). For populations located near a boundary two populations may result, with a separate relationship between SWT and PWT for each. For example, at some point the principal axis describing group 3 simulations, with a gradient of 1.36, must intersect the PHI boundary with its gradient of 0.7. Statistical calculations of simulations allow extrapolation beyond the intersection point so a linear relationship with a symmetrical ellipse is possible. However, the biological limits indicate no plants can lie beyond the intersection of the principal axis and the PHI boundary. The original SWT versus PWT relationship must be modified.

If plants are located in this region then two groups of plants would exist. Those plants with a PWT value below that of the intersection point can be described by the original relationship. For plants with PWT values above the intersection point, the SWT values predicted from the original relationship would be unattainable. This second group of plants therefore have a maximum SWT value defined by the PHI boundary. The boundary consequently also represents the SWT versus PWT relationship of this second group.

It follows that two separate relationships may therefore be necessary to describe the population. That is, a change in mean coordinate could result in an ellipse location further up or down these principal axes. However, the plants in such populations can not be located beyond the PHI limit so the previous linear relationship between SWT and PWT would be lost and the ellipse modified to indicate that the PHI boundary had not been crossed (Figure 4.4).

The PHI values of this second group would then all be about 70 %, provided the relationship between SWT and PWT continues to follow the PHI boundary. In contrast, the PHI values from the first group will be less than 70 %. As a consequence a bimodal PHI distribution may result. The effects of boundary conditions on PHI values are discussed in greater detail in Section 4.5.

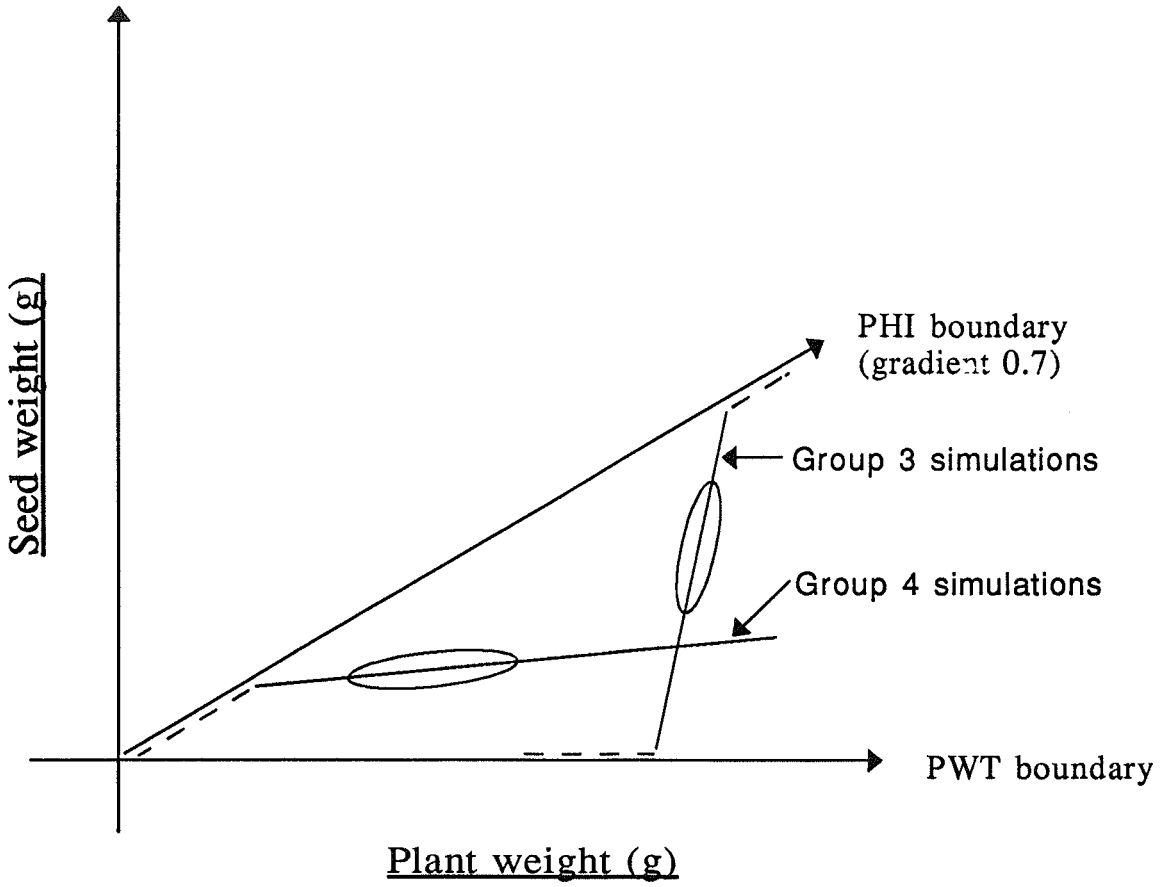
In a similar manner, as the population of plants represented by an ellipse approaches the PWT axis boundary, the population must be modified because no individual plant may lie beyond the PWT axis. The normality of PWT distributions may consequently be lost. For example, PWT distributions from plants grown in highly competitive environments have often been reported as positively skewed with a disproportionate number of small plants (Waller, 1985; Petersen *et al.*, 1990). In terms of the ellipse, this increased positive skewness would cause the mean coordinate to be shifted to the left of the center of the ellipse and, as a result, the mean would be relatively closer to the lower apex.

Where calculations from the PAM indicate that part of the ellipse lies outside one or more of the boundaries, the ellipse should be modified to coincide with the boundary. Consequently, the symmetry of the ellipse would be lost and, the simple ellipse plus principal axis model would require modification.

In summary, the biological limits are physiological constraints on the theoretical model. Plants cannot lie outside these boundaries, by definition, but unusually distributed populations can artificially cause part of the statistical distribution to fall outside these limits and therefore be unrealistic. When this occurs the PAM needs to be constrained within these limits.

Figure 4.4: The effect of PHI and PWT axis boundaries on the gradients of the principal axes, as illustrated for simulations in groups 3 and 4.

Note: The region where the principal axis is modified by a boundary is given by a dashed line (---).



4.4.3 Boundary Conditions and Simulations

The FD values of the initial 16 simulations were chosen to ensure the ellipses were either wholly inside or outside these boundaries. Two further simulations were performed to examine the theoretical effects of the boundary conditions on the components of the model. Simulations Q and R represent a population of plants located closer to the origin, and therefore under greater influence from the PWT and PHI boundaries, than the initial simulations (A-P). For simulation Q no constraints from the boundaries were applied. However, for simulation R this population was modified to lie within the boundaries.

The PWT population had a mean of 1.3 g and a SD of 0.7 g, and the corresponding SWT values were again obtained from Equation 4.3. These PWT values were arbitrarily chosen to illustrate the impact of the boundaries. Other PWT values could have been used provided the initial simulation produced some coordinates that were outside the boundaries. Clearly these simulations represent a crop which cannot occur in practice.

4.4.3.1 Simulation Q. Simulation Q was run under the same conditions as the original 16, with no constraints placed on SWT or PWT values (i.e. negative values were permitted) and the correlation coefficient was maintained at 0.91.

The data generated from this simulation included three PWT and 27 SWT values which were negative (Figure 4.5Q). The mean calculated PWT was 1.3 g with a SD of 0.66 g, and the mean and SD for SWT were 0.26 g and 0.426 g respectively (Table 4.2). The principal axis retained a similar position to that in simulation A, with the same gradient and an intercept of -0.58 (Table 4.2). The resulting ellipse had a similar axes ratio to simulation A, but the projected lengths on both axes were reduced in proportion to the lower SD values (Table 4.2).

4.4.3.2 Simulation R. For simulation R, data was generated to illustrate the effects of the boundary conditions by using the same data set as simulation Q. However, for simulation R the negative values were replaced with zeros. The data set was therefore modified to include 27 barren plants (PHI=0) and three plants represented by the coordinate (0,0), which could be considered as plants that died within the population (Figure 4.5R).

With these barren and dead plants included, the FD values from simulation R retained a mean PWT of 1.33 g and a SD of 0.65 g (Table 4.2). However, the mean SWT increased to 0.33 g and the SD dropped to 0.341 g due to the removal of the negative values. The principal axis showed a clockwise rotation with the slope decreasing from 0.62 in simulation A to 0.48, and in simulation R the SWT axis intercept increased to -0.32 g (Table 4.2). In addition, the correlation coefficient decreased to 0.86.

The projected length on the SWT axis decreased from 1.38 g for simulation Q to 1.08 g for simulation R. However, the SWT coordinate from the lower apex of ellipses from both simulations Q and R was calculated as a negative value, and therefore below the PWT axis boundary. In reality, no points can lie below this axis so neither the ellipse nor any individual point should extend beyond this or any other boundary.

The ellipse for simulation R was therefore restricted to contain data within the boundary limits. As a consequence the elliptical shape and symmetry about the principal axis was lost (Figure 4.5), and the projected length on the PWT and SWT axes decreased to 0.95 and 0.85 g respectively (Table 4.2).

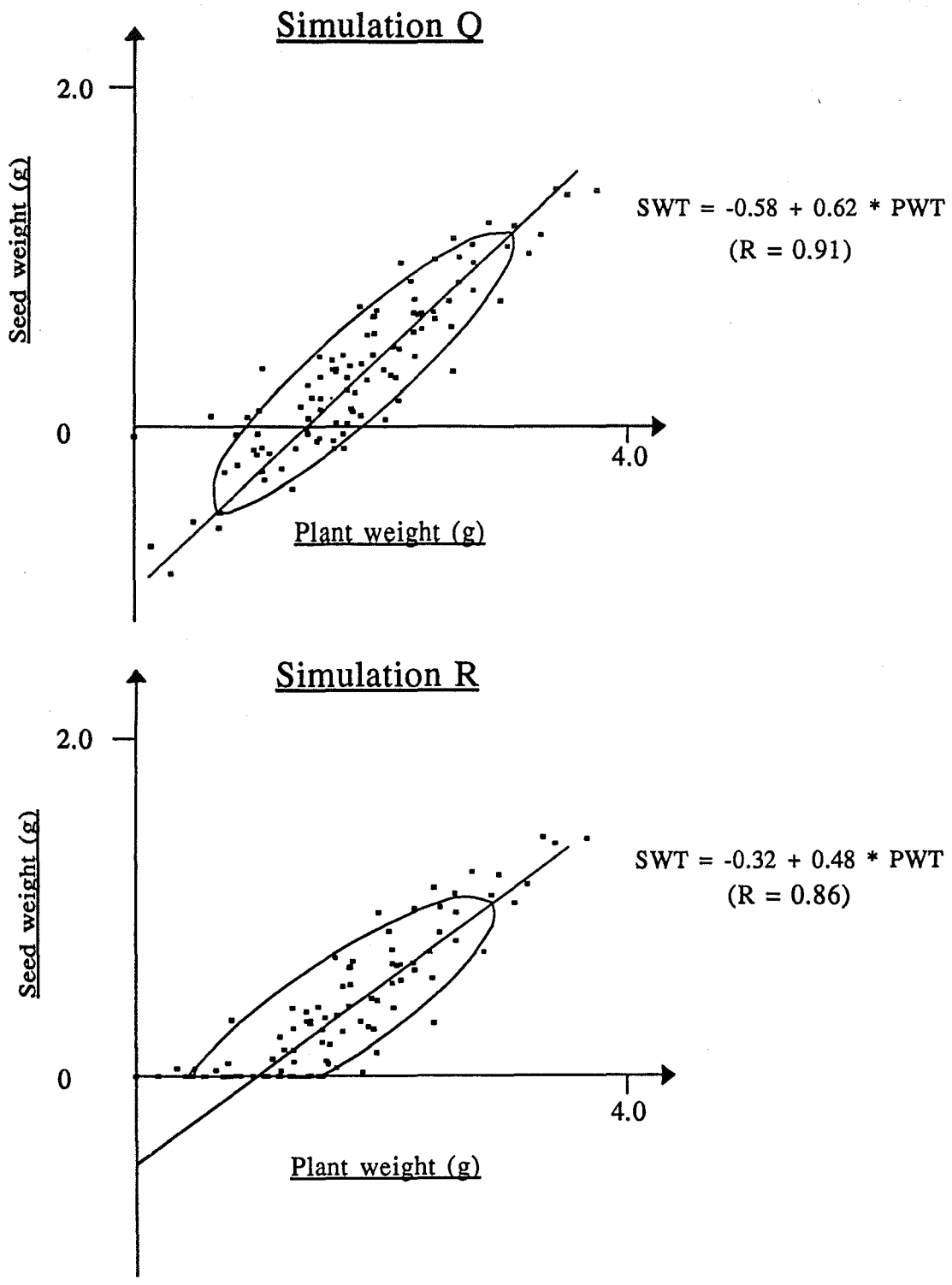
The effect of the boundary condition was therefore to create a clockwise rotation of the principal axis between simulations Q and R. This was analogous to the results reported for simulations in group 4 (Section 4.3.2.3), where only the SD for PWT was increased. The comparisons of simulations Q and R therefore supports the initial interpretation of group 4 results, that when the SD for SWT decreases relative to the SD for PWT, clockwise rotation of the principal axis is expected.

Table 4.2: Relationship between simulated data sets with varying correlation coefficients (R) and their derived principal axis and ellipse values. The mean PWT and SWT values are given as $\overline{PWT}$ and $\overline{SWT}$. The SD values for SWT and PWT are represented by PWT_{sd} and SWT_{sd}.

Simulation	Frequency distribution values (g)				Principal axis values			Ellipse values		
								Projected lengths (g)		Axes ratio
	$\overline{PWT}$	$\overline{SWT}$	PWT_{sd}	SWT_{sd}	Intercept (g)	Gradient	(R)	PWT	SWT	
Q	1.33	0.26	0.66	0.43	-0.57	0.62	0.91	2.21	1.38 (0.95)*	5.19
R	1.33	0.33	0.65	0.34	-0.32	0.48	0.86	2.16	1.08 (0.85)	4.51
S	10	5.4	0.95	0.95	-4.71	1.00	0.56	2.82	2.82	1.88
T	10	5.2	0.95	1.11	-8.06	1.32	0.56	2.65	3.48	1.94

KEY: **Values in parentheses represent projected lengths on the SWT axis after negative values were removed from simulations.*

Figure 4.5: Relationship between seed weight and plant weight, and the resulting components of the PAM from simulations Q and R. (R is the correlation coefficient).



4.4.4 Correlation Coefficients and Simulations

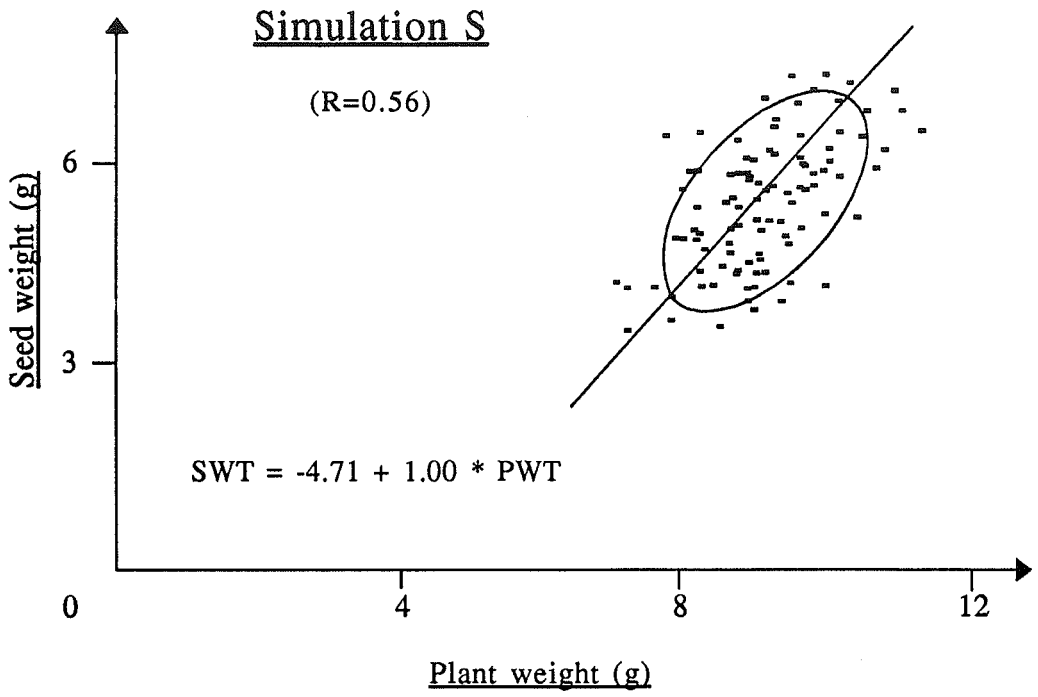
The correlation coefficient was maintained at 0.91 in the first 17 simulations and was only relaxed when the data set was modified for simulation R. Two final simulations were conducted to examine the effects of changes in the correlation coefficient on the model components.

4.4.4.1 Simulation S. For simulation S the 100 randomly generated points for PWT were the same those used for simulation A. The mean and SD values for PWT in simulation S were therefore identical to those in simulation A. To alter the correlation coefficient for simulation S the SWT values were again obtained from Equation 4.3 but the error term was altered to produce a correlation coefficient, arbitrarily chosen to be 0.56. This value was substantially lower than the correlations found in Chapter 3.

The resulting SWT population had a similar mean (5.4 g) but a higher SD (0.95 g) than those reported for simulation A (Table 4.2). Two values had SWT coordinates above the PHI boundary and were adjusted to give a PHI of 70 %. The principal axis had a slope of 1.00 and a SWT axis intercept of -4.7 g. Effectively, these changes in the principal axis represented an anti-clockwise rotation from the control position (Figure 4.6). The axes ratio dropped to 1.88 which reflected the increased variance along the minor axis while the projected length on each axis was equal at 2.82. Compared to simulation A, the projected lengths represented a decrease on the PWT axis but an increase on the SWT axis (Table 4.2).

In summary, the decreased correlation coefficient for simulation S was associated with an increase in the variance along the minor axis and in an increase in the SD for SWT. As a consequence, when compared to simulation A, the principal axis of simulation S had rotated anti-clockwise with a decrease in the SWT axis intercept. Over all the effect on the principal axis of this change in the correlation coefficient could be predicted from the group 3 simulations.

Figure 4.6: Relationship between seed weight and plant weight, and the resulting PAM components from simulation S. (R is the correlation coefficient).



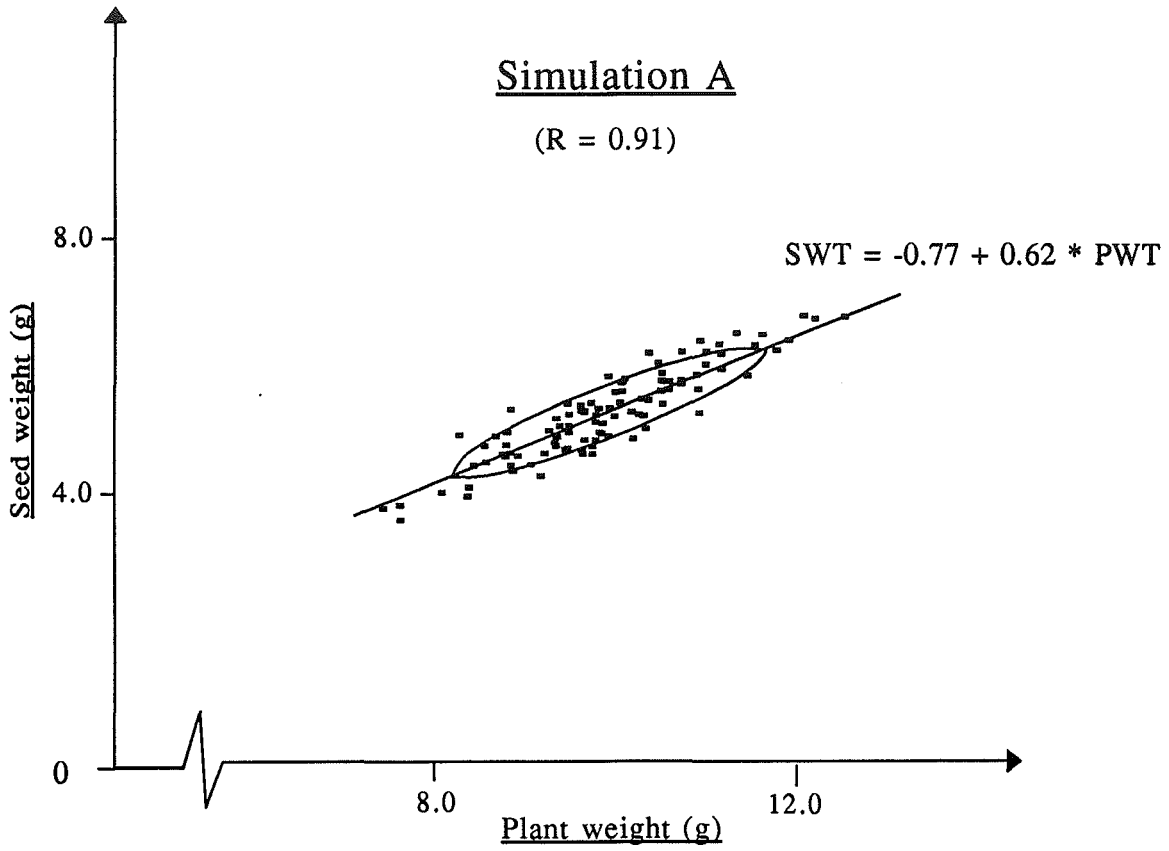
4.4.4.2 Simulation T. In the final simulation the data set was modified, to include poor performing plants (PHI $\leq$33 %), similar to those reported for the field data in Section 3.2.2. In simulation T, the SWT values for a random selection of 10 % of the data in simulation A were reduced (Figure 4.7). The result was a reduction of the correlation coefficient to 0.56 (Table 4.2).

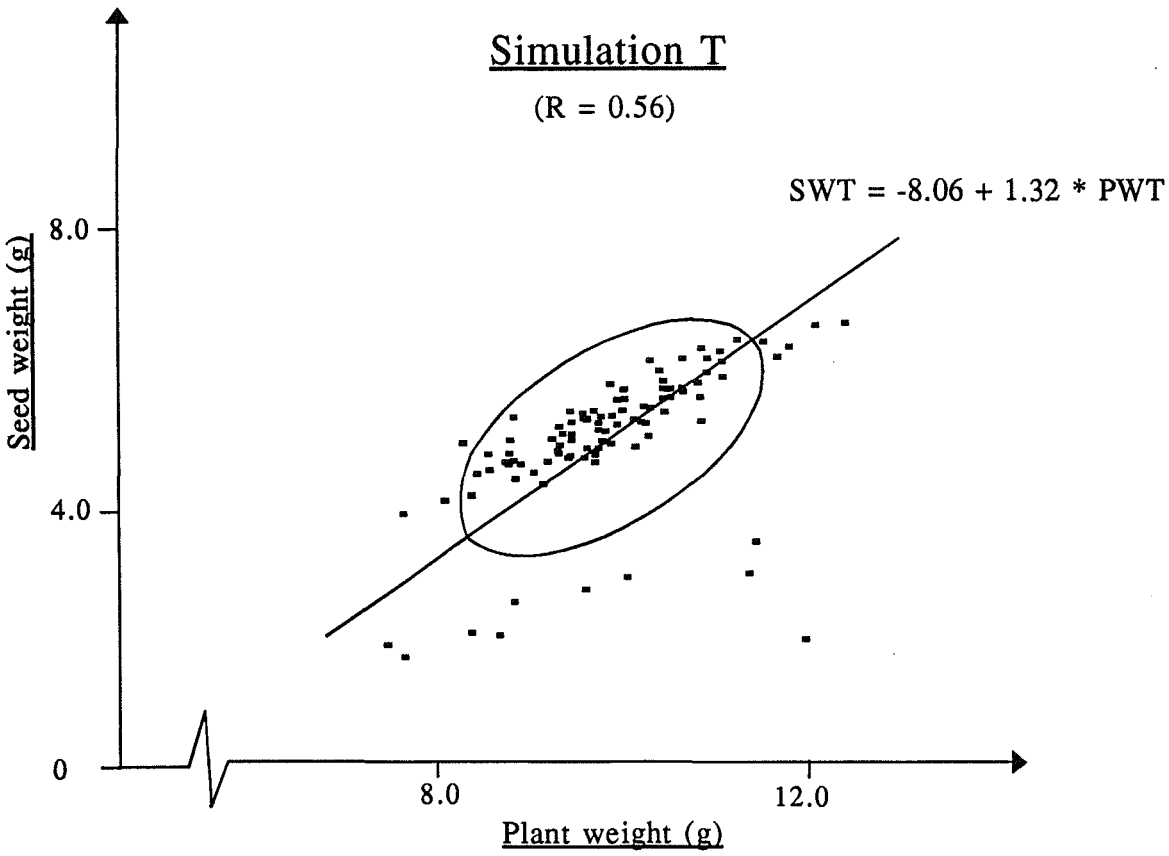
In simulation T, the FD values for PWT were unchanged from the control but the mean SWT dropped from 5.5 g to 5.2 g and the SD increased from 0.61 g to 1.11 g. The effect on the model components could again be predicted from group 3 simulations, with an anti-clockwise rotation of the principal axis to a slope of 1.32 and a decrease in the SWT axis intercept to -8.06 g. The axes ratio of 1.94 indicates an increase in variance along the minor axis and also that the internal area of the ellipse had increased relative to simulation A (Figure 4.7).

4.4.4.3 Summary of simulations Q to T. Thus, in summary the results from simulations Q to T show that the components of the PAM could be used to identify the effects of a change in the correlation coefficient for the relationship between SWT and PWT. The major conclusion from simulations Q to T was that the changes caused by the boundary conditions and in the correlation coefficients were reflected in changes in the FD values of SWT and PWT. Therefore, the effects on the principal axis and ellipse of these changes could be predicted from the initial 16 simulations, provided an adjustment of the ellipse shape was made to prevent the boundaries being crossed.

Many factors may affect the growth and development of a plant within a crop. However, the results from these 20 simulations indicate that, provided the FD values for SWT and PWT can be estimated, the variation in individual plant performance in a crop can be described using the PAM.

Figure 4.7: Relationship between seed weight and plant weight, and the resulting PAM components from simulations A and T. (R is the correlation coefficient).





4.5 MODEL COMPONENTS AND PHI

The second major phase of developing the PAM was to examine the implications for PHI of changes in the FD values of SWT and PWT and the model components. The following discussion initially focuses on how to estimate FD values for PHI (Section 4.5.1, 4.5.2), and then uses these estimates to interpret the effects of changes in the ellipse location (Section 4.5.2.1) and size (Section 4.5.2.2) on the PHI values. Some general comments are then made about the combined effect of changes in both the location and size of the ellipse (Section 4.5.2.3) and, finally, the influence of rotation of the principal axis on PHI values is discussed (Section 4.5.2.4).

4.5.1 Principal Axis and PHI

The PHI values for a population of plants can be related to the principal axis of the PAM by combining Equation 4.1 with Equation 4.3 (after the E_{ij} term used to create variability in the simulations is dropped) to give:

$$PHI = b + a/PWT \qquad \text{(Equation 4.9)},$$

where *a* is the SWT axis intercept and *b* is the slope of the principal axis.

Results in Chapter 3 (Section 3.2.4) showed that the SWT axis intercepts (*a*) were negative for all 12 crops, and that plants with the lowest PHI values tended to have lowest PWT values. These two observations were interpreted as evidence that a MPW is required for seed production in field peas. The MPW was estimated by calculating the PWT value when the SWT was zero, or the PWT axis intercept (MPW = $-a/b$).

The implications of a negative SWT axis intercept ($-a$) and subsequent calculation of a MPW can be interpreted from Equation 4.9. As PWT values decrease the consequent

'-*a*/PWT' term in Equation 4.9 increases and lower PHI values result. For example, using the principal axis values from simulation A (Table 4.2A), a 10 g plant has a predicted PHI of 54.3 % compared to 46.6 % for a 5 g plant, as follows:

(10 g plant) PHI = 0.62 - 0.77/10
= 0.543 or 54.3 %.

(5 g plant) PHI = 0.62 - 0.77/5
= 0.466 or 46.6 %.

Thus, crops with a high proportion of small plants may consequently have a lower mean PHI. Hedley and Ambrose (1981) have reported a similar relationship between PHI and PWT for field peas, as have Gardner and Gardner (1983) for large seeded species in general.

Alternatively, if the SWT axis intercept is zero, then the principal axis must pass through the origin so both the '-*a*/PWT' and MPW terms are zero. With a MPW of zero, both the 5 g and 10 g plants in the previous example would have PHI values of 62 %. That is, with no MPW, every plant would have a PHI value equal to the gradient (*b*) of the principal axis regardless of its PWT.

Positive SWT axis intercepts can also be calculated for the SWT versus PWT relationship. However, a positive SWT axis intercept exceeds the PHI boundary so the population would be modified, as outlined in Section 4.4.2, to give a maximum intercept of zero (Figure 4.4).

4.5.2 Calculation of PHI Values

The influence of a negative intercept, and therefore existence of a MPW, can be examined by considering the effects of changes in the FD values on PHI values. To do

this, the FD values reported for the first simulation were again used to define the control crop and the initial positions of the principal axis and ellipse (Table 4.1A; Figure 4.2A). Equations 4.10 and 4.11 provide solutions for the mean and SD values of PHI for crops simulated from changes in FD values of SWT and PWT (Mood, *et al.*, 1974):

$$E\left(\frac{SWT}{PWT}\right) = \frac{SWT_m}{PWT_m} - \frac{1}{PWT_m^2} \times COV + \frac{SWT_m}{PWT_m^3} \times PWT_v \qquad \text{(Equation 4.10)}$$

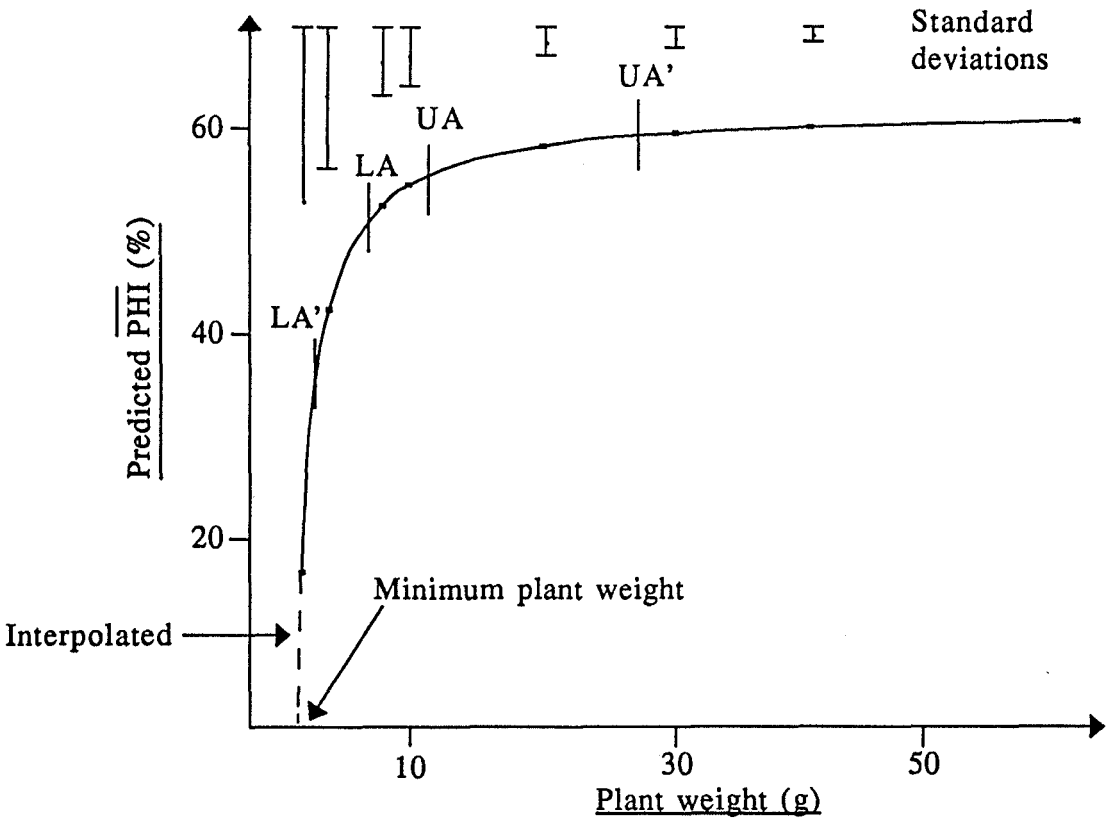
$$VAR\left(\frac{SWT}{PWT}\right) = \frac{SWT_m^2}{PWT_m^2}\left(\frac{SWT_v^2}{SWT_m^2} + \frac{PWT_v^2}{PWT_m^2} - \frac{2COV}{SWT_m \times PWT_m}\right) \qquad \text{(Equation 4.11)}$$

where SWT_m, SWT_v, PWT_m and PWT_v are the mean and variance for SWT and PWT respectively, and COV is the covariance of SWT and PWT. Equation 4.10 differs from Equation 4.9 in that it incorporates data for the variation of SWT and PWT populations in the estimate of mean PHI. A comparison of mean PHI results from these two equations is given in Appendix I and these generally differed less than 1 %. For analyses in this chapter, Equations 4.10 and 4.11 were used to estimate FD values for the PHI populations. Equation 4.9 was not used.

4.5.2.1 Ellipse location and PHI. The PHI values from simulation A were a mean of 54.3 % and a SD of 2.16 % (Table 4.3). These values are used as a base for PHI results to which PHI values from other simulations are compared. The SWT axis intercept and slope were -0.77 g and 0.62 respectively, which gave a calculated MPW of 1.24 g for this control position. To determine the effect of the MPW, PHI values were calculated using Equations 4.10 and 4.11 for a series of populations with the same principal axis and ellipse parameters as simulation A. The mean values for these populations were successively changed from 2 g to 60 g in 2 g increments, and from these populations an overall PHI response to the increases in mean PWT was estimated

Figure 4.8: Predicted mean PHI values from simulation A versus mean PWT.

Note: LA and UA = the position of the lower and upper apex of the ellipse from simulation A. LA' and UA' are the hypothetical apex positions for the lower and upper apex of the ellipse from a comparison crop (Section 4.5.2.2)



(Figure 4.8). The starting point of 2 g was chosen to exceed the MPW (1.24 g) and thus ensure that all calculated mean PHI values were positive. The PHI response between PWT values of 1.24 and 2.00 g were found by interpolation.

The mean SWT values which corresponded to these PWT values were predicted from the principal axis of simulation A. Graphically, this series of populations represents a series of ellipses with the same dimensions, located at varying positions (defined by the changing mean coordinate) along the same principal axis as found for simulation A.

As the mean PWT increased from 2 to 10 g (or to the control position), mean PHI values increased substantially from 15.5 to 54.3 %. Further PWT increases from 10 to 60 g resulted in a highest mean PHI of 60.7 % and the SD decreased from 2.16 to 0.4 % (Figure 4.8).

Thus, the relationship between PHI and PWT was asymptotic with a declining influence of the MPW as the mean PWT increased. For plants of low dry weight, particularly less than 6 g, the MPW constituted a large proportion of their individual PWT so their PHI values are low. As PWT increases the MPW became a progressively smaller proportion of the PWT and the PHI values increased.

Mathematically this relationship can be seen from rearrangement of Equation 4.9 to:

$$PHI_i = b\left(1 - \frac{MPW}{PWT_i}\right)$$

whereby the effect on PHI of the $-MPW/PWT_i$ is greatest for small plants. The slope of the principal axis (*b*) is the asymptote for the mean PHI which was 62 % for simulation A. This asymptote cannot be attained if the SWT axis intercept is negative. With an intercept of zero, and therefore no MPW, the mean PHI values would be equal to the coefficient for slope of the principal axis and independent of PWT. Figure 4.8 would be

modified to a straight line parallel to the PWT axis at a value equal to the slope of the principal axis for all PWT values.

Figure 4.8 provides the key to interpreting the effects of differences in PWT values between crops on their mean PHI values. Essentially, the parameters describing this response curve will vary between populations. The PWT axis intercept is estimated by the MPW (PHI=0 %) and the upper asymptote is defined by the slope of the PAM.

The effect of the range in PWT values within a population on mean PHI values can be predicted from Figure 4.8. For example, a crop with PWT values from 2 to 10 g is predicted to produce plants with PHI values ranging from 15.5 to 54.3 % (Figure 4.8). In contrast, a population of larger plants spread over a similar range of sizes (e.g. PWT values of 32 to 40 g) will have PHI values ranging from 59.6 to 60.1 % (Figure 4.8), so its mean PHI must be higher. It is recognised that the seed yields per unit area of such crops may be the same because the numbers of plants in the population may be very different, and fully compensate for the PHI differences.

The effect of the asymptotic relationship can also be demonstrated by comparisons of simulations A with D, E with H, I with L and M with P. Within each of these four pairs of simulations the SD values for SWT and PWT, gradients, axes ratio and projected lengths were similar (Table 4.1). Differences in mean PHI within each pair can therefore be related to differences in location of the ellipse. For simulations A,E,I and M, the mean coordinate was (10.0, 5.5) but for D,H, L and P it was (30.0, 17.5). This second coordinate represented a shift up an axis described by Equation 4.3 and resulted in an increase in mean PHI of 3.7, 4.3, 3.7 and 1.9 % for each of the four pairs respectively (Table 4.3). Over all the proposal of increased PHI values with increased PWT, due to a decreased influence of the MPW, was supported.

Further comparisons of simulations A with B, E with F, I with J and, M with N also illustrate the importance of the MPW value. For each of these pairs, the principal axes

have the same slope and the ellipse descriptors are identical (Table 4.1). The effect on mean PHI within each pair of simulations can be explained by their differences in the SWT axis intercepts and MPW values. For example, moving from simulation A to simulation B the mean PWT was increased from 10.0 to 30.0 g, and the mean PHI decreased from 54.3 to 18.1 %. The shift in mean PWT also caused the MPW to increase from 1.24 to 21.6 g, although the slope and SDs for SWT and PWT remained the same. Similar changes occurred for the comparisons of simulations E with F, I with J, and M with N. In all three comparisons the lower SWT axis intercept, and therefore higher MPW, resulted in lower PHI values (Table 4.1).

In summary, when the slope of the principal axis and the correlation coefficient are the same for two populations, the population with the lower SWT axis intercept will have a lower PHI value for every PWT, due to the larger influence of MPW, and therefore also a lower mean PHI. In terms of Figure 4.8, the PHI versus PWT response would be similar within each pair of simulations. However, the simulations with lower SWT axis intercepts have larger MPW values and consequently their PWT axis intercept (PHI=0) is higher.

A third group of comparisons, of simulations A with C, E with G, I with K and M with O highlights the opposite effect. In all cases the SWT axis intercept increases but the principal axes have the same slope (Table 4.1). These comparisons represent the mean SWT increase from 5.5 g to 17.5 g with mean PWT constant at 10.0 g. The ellipse location of these simulations was above the PHI boundary and therefore biologically unrealistic, as indicated by the mean PHI values of approximately 200 % (Table 4.3).

Table 4.3: Relationship between PHI values and apex co-ordinates of the ellipses which resulted from simulations. Values are for the 20 simulations used in development of the PAM. SD is the standard deviation of the PHI values.

Simulation	Plant harvest index (%)		Apex co-ordinates			
			Upper		Lower	
	Mean	SD	PWT	SWT	PWT	SWT
A	54.5	2.59	11.63	6.46	8.46	4.49
B	18.1	1.54	31.63	6.46	28.46	4.49
C	175.0	11.19	11.63	18.46	8.46	16.49
D	58.2	0.85	31.63	18.46	28.46	16.49
E	53.7	5.34	13.14	7.39	6.75	3.34
F	17.7	3.20	33.14	7.39	26.75	3.34
G	178.9	22.67	13.14	19.39	6.75	15.34
H	58.0	1.70	33.14	19.39	26.75	15.34
I	54.6	8.06	11.58	7.64	8.50	3.44
J	18.3	3.61	31.56	7.64	28.50	3.44
K	175.1	7.25	11.58	19.64	8.50	15.44
L	58.3	2.63	31.56	19.64	28.50	15.44
M	56.9	5.73	13.16	6.52	6.73	4.60
N	18.5	1.09	33.16	6.52	26.73	4.60
O	182.1	28.46	13.16	18.52	6.73	16.60
P	58.8	2.06	33.16	18.52	26.73	16.60
Q	9.9	23.16	2.43	0.95	0.22	-0.43
R	19.6	16.43	2.42	0.85	0.25	0[+]
S	53.5	7.87	11.46	6.78	8.63	3.96
T	51.7	9.27	11.37	6.94	8.72	3.46

[+]*Value modified from -0.20 due to the PWT axis boundary.*

4.5.2.2 Major axis of the ellipse and PHI. In this section, the effect of a change in the major axis of the ellipse on the PHI values is considered, when other descriptors are constant. This situation occurs when the SD values for SWT and PWT increase by an equal proportion, so that the axes ratio is constant (Table 4.1, Group 2). The effect on PHI can be examined by defining simulation A as the control position, with Figure 4.8 representing the PHI versus PWT relationship.

In simulation A the mean PHI was 54.5 % when the PWT coordinates of the ellipse apices were at 8.46 and 11.63 g for the LA and UA respectively (Table 4.3). The influence of changes in the ellipse size can be interpreted by defining two hypothetical points, LA' and UA', to represent the PWT value for lower and upper apices of comparison crops with the same principal axes as the control. The LA' and UA' have lower and higher PWT values than LA and UA respectively (Figure 4.8), although the actual PWT values are not important for the discussion which follows (Figure 4.8).

When the upper apex of a comparison crop is the same as the control (UA'=UA) but the lower apex (LA') is below the control (LA), the mean PHI of the comparison crop will be lower than the control. The reduced mean PHI results from the inclusion in the latter example of smaller plants which have progressively lower PHI values (Figure 4.8). The rate of change in the mean PHI accelerates as the LA' coordinate is located further down (closer to the PWT axis intercept) the steep linear phase of the asymptotic relationship.

Conversely, when the PWT value of the lower apices of comparison and control crops are equal (LA'=LA), comparison crops will have a higher mean PHI value when the PWT value for UA' exceeds that from the control (UA). The rate of change in the mean PHI would become smaller as the UA' value is located further along the PWT axis due to the declining rate at which the asymptote is approached.

When the PWT coordinates for both apices of the comparison crop (LA', UA') extend

beyond those from the control (UA, LA), the effect on mean PHI will depend on the relative proportions of plants with low and high PWT values. However, the greater rate of change in PHI values below the LA indicates that smaller plants will have a larger effect on the mean PHI than the larger plants. For example, the apices from simulation E both extend beyond the apex positions from the control and, in this situation, a lower mean PHI was calculated (Table 4.3). The lower mean PHI indicates a greater overall influence of the plants with PWT values below LA than those above UA.

In general, large differences in the mean PHI will only occur when a part or all of the population is located in the initial linear section of the asymptotic relationship between PWT and PHI, where the rate of change in PHI is greatest (Figure 4.8). For example, large variability in PHI values may occur when PWT values are low, as a result of high plant populations.

4.5.2.3 Combined effect of changes in the intercept and ellipse on PHI.

When both the SWT axis intercept and ellipse size alter, the effect on mean PHI is more complex and difficult to predict. The effect then depends on the combined influence of the MPW and the change in proportion of small plants. For example, a comparison crop with a lower SWT axis intercept will have a lower mean PHI than the control if the SWT coordinate of its upper apex is less than, or equal, to that of the control crop. However, the effect on mean PHI is uncertain when the upper apex of the ellipse from the comparison crop extends beyond that from the control, due to the relative contribution to the mean PHI from small and large plants. In simulation F the effect of a larger MPW than simulation A overwhelmed any advantage from its higher upper apex coordinate for SWT as shown by the low mean PHI of only 17.7 % (Table 4.3).

For a comparison crop with a lower MPW (higher PWT axis intercept) but similar gradient, the mean PHI will be higher provided the lower apex has a SWT value equal to, or greater than, that of the control crop. At each PWT value the predicted SWT value from the comparison crop is then higher.

4.5.2.4 Effect of rotation on PHI. Rotation of the principal axis was observed when the changes in the SD for SWT and PWT were not equal (Simulations I-P). Rotation of the principal axis has two effects. Firstly, the potential maximum mean PHI changes due to the change in slope (Section 4.5.2.1) and, secondly, the changes in projected lengths and apex coordinates of the ellipse, influence the importance of the balance between small and large plants.

Anti-clockwise rotation of the axis occurred when the SD of SWT increased while the SD for PWT remained constant. The increased slope means an increase in the potential maximum mean PHI (Simulations I-L; Table 4.1I-L). The calculated slope of 1.36 indicates a theoretical PHI asymptote at 136 % for the relationship between PWT and PHI. This mean PHI is much higher than the realistic maximum and, in practice, the slope would be reduced by the PHI boundary to give an effective PHI asymptote for the mean PHI of 70 %.

The actual mean PHI produced will depend on the combination of slope, SWT axis intercept and ellipse location. For two crops with the same SWT axis intercept and similar ellipse locations the one with the higher slope would have the higher mean PHI. In general, crops with a lower slope for the principal axis have a lower potential maximum PHI.

The effect of clockwise rotation and thus lower gradients for the principal axis can be assessed by comparing simulations in group 4. Simulation O was biologically unattainable with a mean PHI of 182.1 % and can be excluded from the discussion (Section 4.5.2.1). The other three simulations (M,N and P) all had gradients of 0.3 but only simulation N had a negative intercept. Its MPW can be calculated (11.2 g) and the gradient becomes the asymptote for PHI at 30 %. The actual PHI of 18.5 % was less than this asymptote (Table 4.3).

In contrast, simulations M and P had mean PHI values which exceeded 30 % so that the gradient was not the maximum PHI asymptote. This apparent anomaly occurs because these two simulations had positive SWT axis intercepts but ellipses which were located within the boundary limits of the PAM. In practice, the principal axes from simulations M and P intersect the PHI boundary and plants can not exist in the extrapolated region between this boundary and the SWT axis intercept. Thus, the principal axis would be modified to follow the PHI boundary from the intersection point down to the origin.

The plants from simulations M and P, with PWT values below this intersection point would have PHI values of 70 %. For PWT values above the intersection point PHI would actually decrease. The PHI would have a further asymptote at 30 % which exists as the minimum PHI asymptote. That is, when the principal axis has a positive SWT intercept and a gradient less than 0.7, the gradient is an asymptote for the minimum mean PHI (Figure 4.8). By definition, when the gradient exceeds 0.7 from a positive SWT axis intercept, the population always exceeds the PHI boundary and can thus only be theoretical.

4.6 PRINCIPAL AXIS AND LEAST SQUARES METHODS OF REGRESSION ANALYSIS

The ideas used to develop this model were based on the principal axis technique described by Sokal and Rohlf (1981). This technique has also been used to estimate the functional relationship between two variables in Model II regression (Sokal and Rohlf, 1981; Moot and Baruch, 1989). However, in Section 3.1.2.3 it was argued that for regression analyses of SWT against PWT, the least squares method is the appropriate statistical technique (Miller 1986; Sokal and Rohlf, 1981). Therefore, whenever coefficients were calculated from field data (Chapters 3 and 6) the least squares regression technique was used.

The differences between these regression methods may alter the coefficients of the principal axis. Least squares analyses minimize variation between the predicted line and individual points in only the vertical (SWT) direction. In contrast, the principal axis technique minimizes variation in both the vertical and horizontal directions (Sokal and Rohlf, 1981; Moot and Baruch 1989). The predicted line from least squares does not necessarily pass through the apices of the ellipses calculated in the simulations presented in this chapter.

The magnitude of the differences between the two techniques was estimated by comparing coefficients for the 20 simulations calculated from principal axis regression (Tables 4.1 and 4.2) with those from least squares (Appendix I). The deviations between coefficients increased as the slope of the principal axis increased and are reported in Appendix I. For example, the slopes from the principal axis and least squares methods were 0.30 and 0.29 respectively for simulation M, 0.62 and 0.59 for simulation A, and 1.36 and 1.21 for simulation I. A similar pattern was observed for the intercepts (Tables 4.1 and 4.2).

For simulations Q and R the coefficients were similar from both methods. However, for simulations S and T the principal axis technique had gradients approximately double those from least squares and intercepts 18 and 6 times lower. Overall the coefficients from least squares regression were more stable than from the principal axis technique when the correlation coefficient dropped to 0.56 (which was substantially lower than those observed in Chapter 3). However, when the correlation coefficient is low, it may be necessary to examine why the relationship between SWT and PWT has broken down for the crop, rather than emphasizing the actual coefficients from either technique. Situations analogous to this are discussed in Chapter 8.

Despite the small differences in coefficients when the correlation coefficient was high the theoretical concepts developed in this chapter, using the principal axis technique and involving the effects of changes in FD values, are expected to hold for the least squares method. The principal axis and ellipse can therefore be considered as tools for illustrating the consequences of differences in FD values between crops.

4.7 SUMMARY

In this chapter, 20 simulations based on 100 randomly selected data points were used to represent possible changes in the FD values of SWT and PWT distributions. The results were interpreted in terms of changes in the coefficients of a principal axis, and in an ellipse calculated to contain 75 % of the data points which were together defined as the PAM.

The initial 16 simulations showed that all changes in the FD values could be described in terms of the PAM. The model was then expanded to include boundary conditions which accounted for the actual biological limits of SWT, PWT and PHI values for field peas. A further four simulations indicated that the behaviour of crops would be modified by these boundaries but, provided changes could be related back to differences in FD values, the initial 16 simulations could again be utilized to interpret the response of each crop.

The implications for mean PHI of changes in the ellipse and principal axis were then examined. Differences in both the SWT axis intercept and the slope of the principal axis were associated with differences in the mean PHI. A negative SWT axis intercept resulted in calculations of a MPW which was shown to affect the mean PHI. In particular, the MPW was expected to influence the PHI of smaller plants more than larger plants. Consequently, with other parameters equal, crops with a high proportion of small plants were predicted to have lower mean PHI values and greater PHI variability. The slope of the principal axis was shown as an asymptote for the maximum potential mean PHI of a crop. Differences in the slope of the line therefore also indicate differences in the maximum mean PHI for crops when the SWT axis intercept is zero or negative. In contrast, the slope provided a minimum mean PHI asymptote for simulations with a positive SWT intercept and gradient lower than 0.7.

Differences in the size of the ellipse were also related to differences in the mean PHI. The positions of the apices, in relation to the initial steep increase in the PHI versus PWT relationship, were shown to be the key factors for interpreting the overall effect on mean PHI.

A comparison of the principal axis and least squares regression techniques indicated minor differences when the correlation coefficient was high (0.91). However, simulations S and T highlighted the relative stability of coefficients from the least squares technique compared to the principal axis technique, when the correlation coefficient was low (0.56). When large differences are observed between the coefficients from these techniques the causes of the breakdown in the linear SWT versus PWT relationship (which cause the low correlation coefficient) becomes important.

In conclusion, this analysis offers four criteria for analysing differences between crops: the intercept and slope of the principal axis and the location and shape of the associated ellipse. Differences in the mean PHI of crops can be explained by any or all of these components and the relative importance of each may vary between treatments and environments.

Examination of the behaviour of FD values and consequent changes in the four components will help to identify the constraining conditions which operate within a pea crop. Once these constraints are known it should become possible to define environmental and genetic characters which allow optimization of yields. Specifically, comparisons will be possible on how the FD values interact within and between genotypes, and which interactions produce the desirable combination of a high mean and low SD for the PHI distribution in a crop.

In the experiment described in Chapter 5 the performances of test genotypes are compared by forcing and varying the degree of interplant competition in crop communities, through changes in planting populations. The responses in each genotype are examined across

contrasting populations. Several methods of analysis are used to describe this experiment including traditional agronomic techniques, such as yield components analyses (Chapter 5). The shape of SWT, PWT and PHI distributions and the assumptions of the PAM are examined in Chapter 6. The aim of these different approaches is to identify the factors associated with variability in seed yields among crops. The analyses may identify the morphological traits required to maintain a stable high CHI over widely varying plant populations. Alternatively, they may indicate different optimum plant populations for morphologically distinct genotypes.

CHAPTER FIVE

PLANT POPULATION EXPERIMENT (1989/90)

5.1 INTRODUCTION

In this chapter the relationship between plant population and yield is examined using four morphologically distinct genotypes. The objective is to relate differences in seed yield between the genotypes to differences in the components of seed yield (defined in Section 2.2.1). Effectively the objective is to test the second main assumption of this study, *viz.* that the effectiveness of each yield component as a selection criterion is low (Section 1.2).

This chapter begins with a description of the design and crop management procedures for a field experiment grown in the 1989/90 season. This is followed by an outline of the measurements that were made and a discussion of the methods used for data analysis (Section 5.2). The assumptions of analysis of variance (ANOVA) and GXE interactions are explored in Section 5.3. The statistical methods used for estimating heritability and genotypic stability of characters across environments, and for describing the response of yield to changes in population, are also discussed. Yield and harvest index results at both the crop and plant levels of classification are presented in Section 5.4. The components of seed yield are then compared across environments and the results of the GXE interaction, heritability and stability analyses are summarized. Finally, the discussion in Section 5.5 compares the yield responses of genotypes across populations in terms of SWT, PWT and PHI. The suitability of each component of yield as a selection criterion is also discussed by examining the relationship between significant differences in total

seed yield and the yield components, and considering their heritability and stability across environments.

5.2 MATERIALS AND METHODS

5.2.1 Experimental Design

The experiment was sown as a split-plot randomized block design, with the four genotypes as the main plots and five plant populations as the subplots. There were four replicates. The plots were sown by hand, one replicate per day on 23 and 24 September and 9 and 10 October 1989. A frame was used to enable seeds to be sown precisely 'on the square', to achieve population treatments of 9, 49, 100, 225 and 400 plants m^{-2}. These populations were chosen to simulate environments ranging from wide plant spacings with no interplant competition, as used in early generations of breeding programmes, through a commercial population, to a very high population where substantial interplant competition was intended to stress each plant within the crop. The trial area was surrounded by a 6 metre wide buffer crop of field peas cv 'Birte' sown at approximately 100 seeds m^{-2} on 27 September 1989.

5.2.2 Site and Soil Characteristics

The experiment was grown on the N.Z. Institute for Crop and Food Research experiment station at Lincoln, Canterbury. The soil was a deep Templeton silt loam which has an available water holding capacity of about 180 mm per metre of depth (New Zealand Soil Bureau, 1968; Cox, 1978).

The site was in cereal trials in 1988-89. Soil nutrient quic[1]- test results taken on 15 February 1989 were pH=5.3, Ca=6, P=9, K=8, and Mg=20 (Appendix II). Stubble was

ploughed in February 1989 and lime at 2.0 t ha^{-1} was applied in March 1989. The site was fallowed until September when it was rolled, then grubbed and crumbled three times. Trifluralin herbicide at 2.5 l ha^{-1} in 200 l ha^{-1} of water was applied on 19 September 1989 and soil-incorporated by a final harrow and roll cultivation before planting the peas.

5.2.3 Genotype Selection

The initial selection of six genotypes was described in Chapter 3. Four of the genotypes (CVN, CLU, SLU, and SVU) were included in this experiment, to represent both conventional and semi-leafless plant types and the three PHI categories identified in Section 3.3.1.

5.2.4 Plot Sizes

The plot sizes varied between populations (Table 5.1). Each group of five subplots, representing the five plant populations, were sown in a 5 x 5.33 m area. The 9 plants m^{-2} population required a 3 x 5.33 m plot and was therefore randomly assigned to approximately one half of the subplot area. The other four subplots were randomly assigned to the remaining area. Each of the plots from these higher populations was 2 metres long but the width decreased from 2 to 0.7 m as the population was increased (Table 5.1).

5.2.5 Plant Numbers

The total number of seeds sown and plants harvested per plot also varied (Table 5.1). Only 144 seeds (16 x 9 rows) were sown in the 9 plants m^{-2} treatments with 60 (12 x 5 rows) of these harvested for analysis at maturity. At the higher populations, between 196 (49 plants m^{-2}) and 560 (400 plants m^{-2}) seeds were sown, giving a total of 27 520 seeds sown. Approximately, 30 % of the plants produced (7 456 plants) were harvested, with between 100 and 104 taken from each of the plots with plant populations from 49 to 400 plants m^{-2} (Table 5.1).

Table 5.1: Agronomic details of the 1989/90 plant population experiment. Each plot occurred 16 times in the experiment (4 genotypes x 4 replicates). Values are expressed as the width of the plot by its length.

Population (plants m^{-2})	Plot dimensions (m x m)	Plant numbers (per plot)	Plants harvested (per plot)	Guard rows per plot			
				Width		Length	
				Number	(m)	Number	(m)
9	5.3 x 3	16 x 9	5 x 12	2	0.66	2	0.66
49	2 x 2	14 x 14	10 x 10	2	0.28	2	0.28
100	1.4 x 2	14 x 20	8 x 13	3	0.30	3	0.30
225	1.2 x 2	18 x 30	6 x 17	6	0.40	6	0.40
400	0.7 x 2	14 x 40	5 x 20	5	0.25	10	0.50

The number of guard rows per plot increased as population increased, giving a range of between 0.25 and 0.66 m around the harvested area of each plot (Table 5.1). A further 0.2 m of field peas (cv. Birte) was planted with a Hege 90/1 single cone seeder at an approximate rate of 100 seeds m^{-2} around each group of five subplots.

5.2.6 Crop Management

Intensive crop management was used to minimize yield variation caused by agronomic factors. Apart from the pre-plant herbicide application, no weed control was necessary in the 225 and 400 plants m^{-2} treatments. In the lower populations weeds were also controlled by hand-hoeing. No fertilizers were applied.

A sprinkler system was used to apply a total of 200 mm of water in three irrigations during the season. The aim was to schedule irrigations to minimize crop exposure to potential soil moisture deficits exceeding 88$\pm$2 mm (Wilson, 1987). Irrigations were actually applied at potential soil moisture deficits of between 106 and 113mm, with consequent potential yield decreases estimated at about 5 % (Jamieson *et al.*, 1984; Wilson *et al.*, 1985).

The trial was sprayed on three occasions to control downy mildew (*Peronospora pisi* Syd.) and powdery mildew (*Erysiphe pisi* DC> ex ST-AM.). On 13 December 1989 a mixture of fungicides, metalaxyl and mancozeb (Ridomil MZ 72 WP) and penconazole (Topas 100EC), was applied using a compressed air knapsack sprayer. The fungicides were applied in 300 l water ha^{-1} at rates of 200 g ha^{-1} metalaxyl, 1600 g ha^{-1} mancozeb (both to control downy mildew), and 30 g ha^{-1} penconazole (to prevent powdery mildew). On 19 December 1989 the plots were sprayed by helicopter with triadimenol (Cereous 250 EC) at 125 g ha^{-1} to prevent powdery mildew. A final application of penconazole (30 g ha^{-1} in 300 l of water) was made with a compressed air knapsack sprayer on 16 January 1990 to control powdery mildew. The fungicide applications were effective.

Downy mildew was noted on the lower leaves of plants in some plots in early December, but disappeared after application of fungicides. Powdery mildew was observed at low incidence in late December and in mid-January, but was controlled effectively by the fungicide applications.

5.2.7 Measurements

At maturity, plants were hand-cut at ground level and measurements of the number of pod and branches were recorded for each plant. Sixty plants per plot were harvested from the spaced plant treatment and approximately 100 plants per plot from other populations (Table 5.1). All plants were then dried in a forced-draught oven at 70 °C for 48-72 hours. Individual PWT, SWT, seed number per plant and signs of viral or fungal damage were recorded.

Viral damage was primarily caused by cucumber mosaic virus which affected the lowest two plant populations more than the three higher ones. However, Chi-square analysis indicated that the frequency of occurrence was generally the same for the four genotypes at each population (Table 5.2). Yields were therefore calculated on a virus-adjusted basis which removed the yield of, and space occupied by, an infected plant from further analyses. This was particularly relevant to the widely spaced plants in the low population treatment where the ability of the crop to compensate for the infected plants was less than at the higher populations.

Several values were derived from these measurements. Seed and biological yields were calculated from the individual plant data. The CHI was derived as: [seed yield / biological yield] x 100. The numbers of peas per pod, and the average weight of individual seeds, converted to 1000 seed weight (1000 sw), were also calculated for each plant.

Table 5.2: Degree of virus infection (% of plants) for field pea genotypes in the 1989/90 plant population experiment. Chi-square analysis was performed on frequency data but results are presented as percentages to overcome the inequalities in sampling numbers between populations. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different.

Genotype	Population (plants m^{-2})				
	9	49	100	225†	400
CVN	8.8_a	3.8_a	3.4_a	1.5_a	0.8_a
CLU	11.7_a	2.8_a	2.6_a	0.8_b	0.5_a
SVU	10.8_a	3.3_a	1.7_b	0.2_a	1.0_a
SLU	8.3_a	2.8_a	1.7_b	1.9_b	1.5_a
(p value)	0.567	0.885	0.016	0.033	0.504

KEY: †50 % of the cells had expected counts less than 5 and therefore Chi-square analysis may not be valid.

5.3 DATA ANALYSES

Two forms of analysis for yield and yield components were necessary, because of the lack of a universally accepted test for homogeneity of variances. Analysis of variance assumes homogeneity of variance (Ho: $\sigma_1^2=\sigma_2^2=\sigma_3^2=\sigma_n^2$; Ha:variances are not equal) and this is commonly tested using Bartlett's test (Bartlett, 1937). However, Bartlett's test and many others developed to test homogeneity of variances are adversely affected by non-normality, have low power or other serious drawbacks (Box, 1953; Gartside, 1972; Keselman *et al.*, 1979; Sokal and Rohlf, 1981). For example, with Bartlett's test, Type II errors (not rejecting Ho when it is false) increase with platykurtic distributions and Type I errors (rejecting Ho when it is true) increase with leptokurtic distributions. Because of the drawbacks of these tests, and the robustness of analysis of variance, Zar (1984) suggests Bartlett's test should not be performed as a test for homogeneity of variances prior to analysis of variance, but offers no alternatives.

5.3.1 Analysis by Population

The first form of analysis used in this chapter rejected the null hypothesis of equal variances. Variance differences of three to four orders of magnitude were found between populations for some variables, particularly those reported on a per plant basis, in this and later chapters (Table 5.3). Reporting this data on a per unit area basis would reduce the inequality of variances (Table 5.3) but, given that the performance of individual plants at each population was the basic level of investigation throughout this study, this adjustment was not made.

To minimize variance inequalities, genotypic differences were investigated at each population, and genotype means were compared using least significant difference (LSD) tests. This approach was utilized for all variables to maintain continuity throughout the analysis of this experiment.

The mathematical model used for a single population (Steel and Torrie, 1980) was:

$$X_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij} \qquad \text{(Equation 5.1)}$$

where: X_{ij} = the value of a quantitative characteristic of the ith genotype in the jth replicate,

μ = population mean,

α_i = effect of the ith genotype (i=1, 2...g),

β_j = effect of the jth replicate (j=1, 2...r),

ε_{ij} = residual effect.

This approach is a conservative method of analysis that results in the loss of a significance test for both population as a main effect, and the genotype by population (environment) interaction.

Table 5.3: Relationship between plant population and the variance values calculated for variables measured from the 1989/90 experiment.

Variable	Population (plants m^{-2})				
	9	49	100	225	400
Seed yield ($g\ m^{-2}$)	276.0	469.1	521.3	201.5	183.9
Biological yield ($g\ m^{-2}$)	583.6	1242.3	1688.9	700.8	787.0
SWT ($g\ plant^{-1}$)	34.13	1.95	0.52	0.04	0.01
PWT ($g\ plant^{-1}$)	65.61	4.91	1.77	0.16	0.052
CHI (%)	2.49	1.14	1.26	1.48	1.21
PHI (%)	3.14	1.50	2.34	2.20	2.65
Pod number ($plant^{-1}$)	15.6	1.49	0.52	0.068	0.022
Pod number (m^{-2})	1267	3493	4941	3692	3456
Number of peas (pod^{-1})	0.041	0.046	0.139	0.049	0.043
1000 sw (g)	35.8	42.3	87.5	119.7	156.5

5.3.2 Analysis by Split-plot

A significance test for the GXE interaction is central to the investigation of phenotypic stability in genetic studies. This was obtained by the second analysis which is the standard analysis of variance for a split-plot designed experiment (Section 5.2.1), with equal variances assumed (Petersen, 1985). Cochran and Cox (1957) point out that the significance tests applied to this pooled analysis of variance could be questioned because of the inequality of variances. However, they indicated that preliminary

conclusions could be drawn from such data because fully efficient, theoretically sound tests were not available. Lamadji (1991) states that such tests are still not available. Pooled analysis of variance was therefore used despite possible inequalities of variance.

The split-plot analysis followed the mathematical models of Sprague and Federer (1951) and Gordon *et al.* (1972). Their models, used extensively to compare several genotypes over different sites and seasons, include environment as the main plot and genotype as the subplot. In this primarily agronomic study, genotype was the mainplot and plant population (environment) the subplot, so the model required rearrangement. The linear additive model, adapted from Model 1 of Gordon *et al.* (1972), therefore becomes an extension of that used for a single environment and takes the form:

$$X_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \eta_k + (\alpha\eta)_{ik} + \varepsilon_{ijk} \quad \text{(Equation 5.2)}$$

where: X_{ijk} = the value of the quantitative character of the ith genotype, measured in the jth replicate of the kth environment,

μ = population mean,

α_i = effect of the ith genotype (i=1, 2...g),

β_j = effect of the jth replicate (j=1, 2...r),

$(\alpha\beta)_{ij}$ = the interaction of the ith genotype and the jth replicate,

η_k= effect of the kth environment (k=1, 2...e),

$(\alpha\eta)_{ik}$ = the interaction effect of the ith genotype with the kth environment,

ε_{ijk} = residual effect.

Using this model, the values of g and r were 4 and e was 5, for this experiment.

Based on this additive linear model, where genotype and environment were not chosen at random, the appropriate data analysis would use the fixed effects model. However, the genotypes were selected for the maximum diversity of morphological characteristics with

no selection on the basis of yield or yield component values, either for the genotypes, environments or their interactions. Furthermore, the plant populations could be considered representative of those within commercially sown field pea crops. The analysis of variance and its expected mean square results are presented in Table 5.4. In using this random effects model it is recognised that the results of the GXE analysis may be restricted to the genotypes included in the study with limited extrapolation to other genotypes or environments possible.

When genotype and environment were chosen as fixed variables and replication as the random variable, the mean squares and expected mean squares were as given in Table 5.4.

Table 5.4: Mean squares and expected mean squares of a pooled analysis of variance for a split-plot designed experiment.

Source of variation	Degrees of freedom	Mean square	Expected mean square
Replicate (R)	r-1	MS6	
Genotype (G)	g-1	MS5	$\sigma^2 + e\sigma_r^2 + r\sigma_{ge}^2 + re\sum\alpha_i^2/(g-1)$
R X G	(r-1) (g-1)	MS4	$\sigma^2 + e\sigma_r^2$
Environment (E)	e-1	MS3	$\sigma^2 + r\sigma_{ge}^2 + \frac{rg\sum\eta_k^2}{(e-1)}$
G X E	(g-1) (e-1)	MS2	$\sigma^2 + r\sigma_{ge}^2$
Error	g(r-1) (e-1)	MS1	σ^2

The significance of the genotype and replicate effects were tested against the genotype by replicate interaction term (MS6 and MS5 against MS4) with 3 and 9 degrees of freedom respectively (Petersen, 1985). The GXE interactions were considered significant if MS2/MS1 was greater than the tabled $F_{0.05}$ value with the corresponding degrees of freedom (12,48).

For the variables considered, variance components were calculated as:

1) Genotypic variance (σ_g^2) = (MS5-MS4-MS2+MS1) /re
2) GXE interaction variance (σ_{ge}^2) = (MS2-MS1) /r
3) Phenotypic variance (σ_p^2) = $\sigma_g^2 + \sigma_{ge}^2 + \sigma_e^2 + \sigma_r^2 + \sigma^2$
4) Broad sense heritability (h^2bs) = σ_g^2 / σ_p^2

5.3.3 Analysis of Phenotypic Stability

Characters showing a significant GXE interaction effect were evaluated for stability using the regression model of Finlay and Wilkinson (1963). With '*g*' genotypes tested in '*e*' environments, the stability model takes the form:

$$Y_{ik} = m + b_i I_k + d_{ik} \quad (i=1, 2...g;\ k=1, 2...e) \quad \text{(Equation 5.3)}$$

where: Y_{ik} = mean of the ith genotype (g=4) in the kth environment (e=5),

m = mean of the ith genotype over all environments,

b_i = regression coefficient of the ith genotype on the environmental index, which measures the response of this genotype to varying environments,

I_k = the environmental index, which is defined as the deviation of the mean of all genotypes in a given environment from the overall mean,

d_{ik} = the deviation from the regression line of the ith genotype in the kth environment.

Table 5.5: Mean harvest index values (%) for the field pea genotypes sown at five populations in the 1989/90 experiment. †Environmental means were used as the independent variable for analyses of stability. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different.

	Crop harvest index				
	Population (plants m^{-2})				
Genotype	9	49	100	225	400
CVN	59.0_a	60.1_a	58.1_b	58.0_a	54.0_c
CLU	59.4_a	61.5_a	61.0_a	59.0_a	58.2_a
SVU	56.9_a	58.5_b	57.9_b	54.6_b	53.4_c
SLU	57.8_a	58.5_b	58.4_b	58.0_a	56.2_b
(SEM)	0.79	0.53	0.56	0.61	0.55
†Environmental mean	58.3	59.6	58.9	57.4	55.5
	Plant harvest index				
Genotype					
CVN	58.3_a	59.4_a	57.0_a	55.1_a	45.9_c
CLU	58.6_a	61.1_a	60.3_a	57.3_a	53.9_a
SVU	56.7_a	58.2_a	57.6_a	52.5_b	50.2_b
SLU	57.5_a	57.9_a	57.2_a	55.1_a	52.1_{ab}
(SEM)	0.89	0.61	0.76	0.74	0.81
†Environmental mean	57.8	59.2	58.0	55.0	50.5

The regression coefficient of each genotype was used as an indicator of stability and adaptation (Finlay and Wilkinson, 1963) for each characteristic tested. Because the individual genotype mean values are regressed against the mean of all genotypes the population mean has a regression coefficient of 1.0. Genotypes characterised by

regression coefficients close to 1.0 have average stability, and they were considered to be either poorly or well adapted to all environments depending on the values of their genotype mean (Yothasiri, 1985). Genotypes with regression coefficients significantly greater than one (b>1) were sensitive to environmental change, and therefore below average in stability. Conversely, genotypes with regression coefficients lower than one (b<1) were insensitive to environmental change, and above average stability. Regression coefficients not significantly different from zero (b=0) indicated little genotypic response to environmental changes.

5.3.4 Regression Analysis of Dry Weight

Least squares regression analysis of mean PWT versus plant population (P) was also calculated. Generally, as plant population increases the mean PWT ($\overline{PWT}$) decreases. The relationship is not linear, and regression of $1/\overline{PWT}$ against the populations produces a linear relationship of:

$$1/\overline{PWT} = A + B(P) \quad \text{(Equation 5.4)}$$

Taking the reciprocal of both sides:

$$PWT = 1/[A + B(P)]$$

This reciprocal model assumes that there is an asymptotic relationship between the biological yield per unit area and plant population (Willey and Heath, 1969). Since: biological yield = $\overline{PWT}$ x P, when P is very high the biological yield can be estimated from 1/B, and this represents the yield potential of the environment. Thus, regression analysis of the inverse of $\overline{PWT}$ against plant population can be used to estimate the expected maximum biological yield of the environment for each genotype. Analysis of covariance was used to compare the slope of these relationships (Snedecor and Cochran,

1980) and therefore give an indication of any differences between genotypes for this expected maximum biological yield for the genotypes in this study.

When the plant population is near zero (spaced plants) the $\overline{PWT}$ can be estimated as 1/A, and this represents the genetic potential of a plant grown without significant competition (Holliday 1960a; 1960b; Willey and Heath, 1969). A comparison of the estimates of 1/A with the mean values at 9 plants m^{-2} was therefore used to give an indication of the level of competition experienced by the plants sown at this population.

5.3.5 Competition Index

The extent of interplant competition within each crop was also quantified by calculating a competition index (CI) as proposed by Weiner *et al.*, (1990). This index compares the plant of highest dry weight from a crop with the $\overline{PWT}$ of the same genotype at 9 plants m^{-2}.

$$CI = \text{largest plant in a crop} / \overline{PWT} \text{ at 9 plants } m^{-2} \times 100/1 \quad \text{(Equation 5.5)}$$

If competition was one-sided (Ford and Diggle, 1981), the largest plants at high populations would be a similar size those from spaced plants, and the CI would be about 100.

5.4 RESULTS

5.4.1 Seed Yields

The seed yield of all genotypes was lowest at 9 plants m^{-2} and almost doubled to around 675 g m^{-2} as the plant population increased to 100 plants m^{-2} (Figure 5.1). Significant differences ($p<0.01$) between genotypes were only found at 225 plants m^{-2}, where genotype CLU (716 g m^{-2}) produced a greater seed yield than SVU (636 g m^{-2}), and at 400 plants m^{-2} where genotypes CLU (784 g m^{-2}) and SLU (781 g m^{-2}) out-yielded ($p<0.01$) SVU (701 g m^{-2}) which in turn had a higher ($p<0.01$) seed yield than CVN (620 g m^{-2}).

5.4.2 Biological Yield

The biological yield of the four genotypes showed similar responses to population up to 100 plants m^{-2}, with biological yield almost doubling (Figure 5.2). From 100 to 400 plants m^{-2} the total biological yield of genotype CVN declined from 1200 to 1145 g m^{-2}. In contrast, the biological yield of the other three genotypes increased by about 200 g m^{-2}. This increase resulted in a significantly ($p<0.01$) lower biological yield for genotype CVN at 400 plants m^{-2} (Figure 5.2).

5.4.3 Crop Harvest Index

There were no CHI differences among the genotypes at 9 plants m^{-2} (Table 5.5). The CHI was highest at 49 plants m^{-2} for all genotypes, with the maximum values ranging from 61.5 % for CLU down to 58.5 % ($p<0.05$) for the two semi-leafless genotypes. The decline of CHI at higher populations varied among genotypes and ranged from 2.3 % (SLU) to 6.1 % (CVN). Genotype SVU had the lowest CHI at all populations and, although it produced its highest seed yield at 400 plants m^{-2} (Figure 5.1), its CHI was lowest (Table 5.5) at 400 plants m^{-2}.

Figure 5.1: Mean seed yield versus plant population for the four genotypes sown in the 1989/90 experiment. Error bars refer to standard errors of the mean.

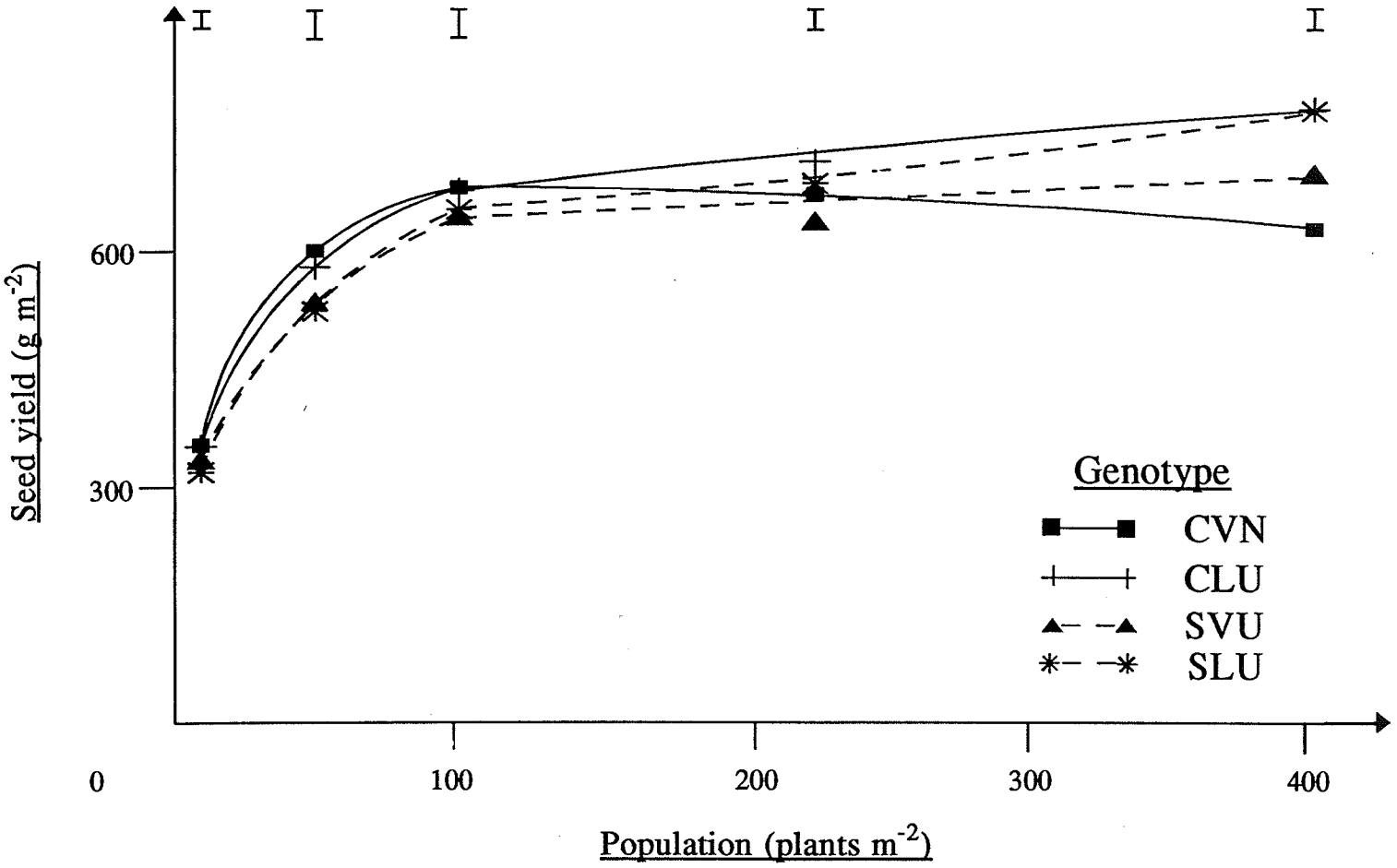
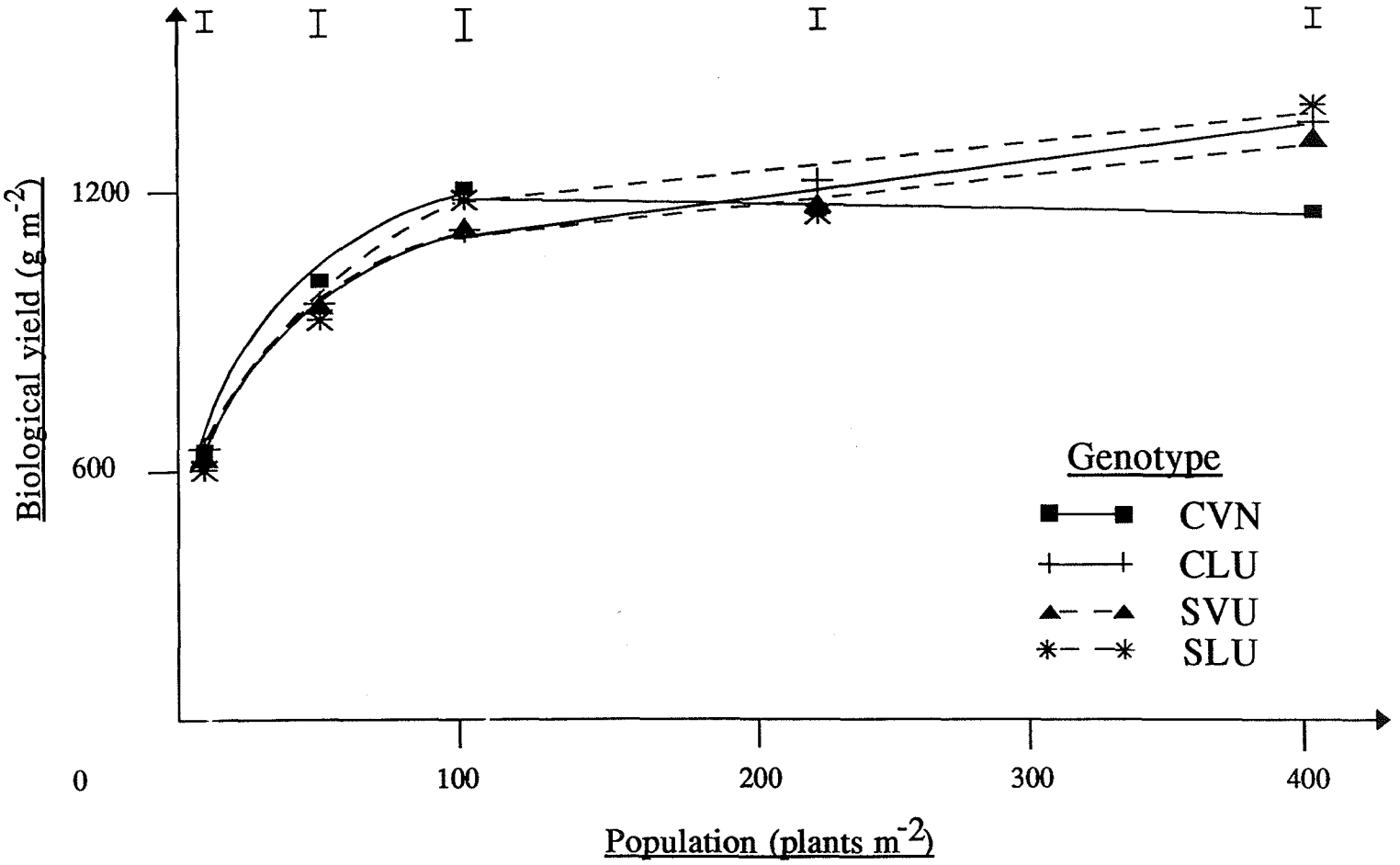


Figure 5.2: Mean biological yield versus plant population for the four genotypes sown in the 1989/90 exeriment. Error bars refer to standard errors of the mean.



5.4.4 Mean Seed and Plant Weights

Mean seed and plant weights decreased about 20-fold from the lowest to the highest populations (Table 5.6). The largest decrease was between 9 and 49 plants m^{-2}. There were no significant differences among genotypes for either mean SWT or PWT from 9 to 100 plants m^{-2}. However, at 225 plants m^{-2} the mean SWT of SVU (2.83 g $plant^{-1}$) was lower ($p<0.01$) than from CLU (3.18 g $plant^{-1}$). At 400 plants m^{-2}, genotype CVN had lower mean SWT and PWT values than the other genotypes ($p<0.05$). Also at 400 plants m^{-2} genotype SVU had a lower ($p<0.01$) mean SWT than both CLU and SLU (Table 5.6).

Table 5.6: Mean SWT and PWT values (g $plant^{-1}$) for field pea genotypes sown at five populations in the 1989/90 experiment. Data are from the 1989/90 plant population experiment. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different.

	Seed weight				
	Population (plants m^{-2})				
Genotype	9	49	100	225	400
CVN	39.8_a	12.2_a	6.97_a	2.96_{ab}	1.55_c
CLU	40.4_a	11.8_a	6.74_a	3.18_a	1.96_a
SVU	37.3_a	11.2_a	6.44_a	2.83_b	1.75_b
SLU	36.3_a	10.8_a	6.85_a	2.94_{ab}	1.95_a
(SEM)	2.92	0.70	0.361	0.100	0.054
	Plant weight				
Genotype					
CVN	70.2_a	20.6_a	12.4_a	5.43_a	3.00_b
CLU	69.7_a	19.6_a	11.5_a	5.64_a	3.51_a
SVU	69.7_a	19.8_a	11.8_a	5.48_a	3.50_a
SLU	62.9_a	18.9_a	12.0_a	5.43_a	3.69_a
(SEM)	4.05	1.11	0.67	0.198	0.114

5.4.5 Mean PHI

The mean PHI values from 9 to 100 plants m^{-2} were similar to the CHI values (ranging from 56.7 to 61.1 %) with no significant differences between genotypes (Table 5.5). At 225 plants m^{-2} the mean PHI for genotype SVU was the lowest ($p<0.01$) at 52.5 %. The mean PHI values for all genotypes were lowest at 400 plants m^{-2} as indicated by the environmental mean of 50.5 % compared to over 55 % at the lower populations (Table 5.5). Genotype CVN produced the lowest ($p<0.01$) mean PHI (45.9 %) while SVU also had a lower ($p<0.01$) mean PHI (50.2 %) than CLU.

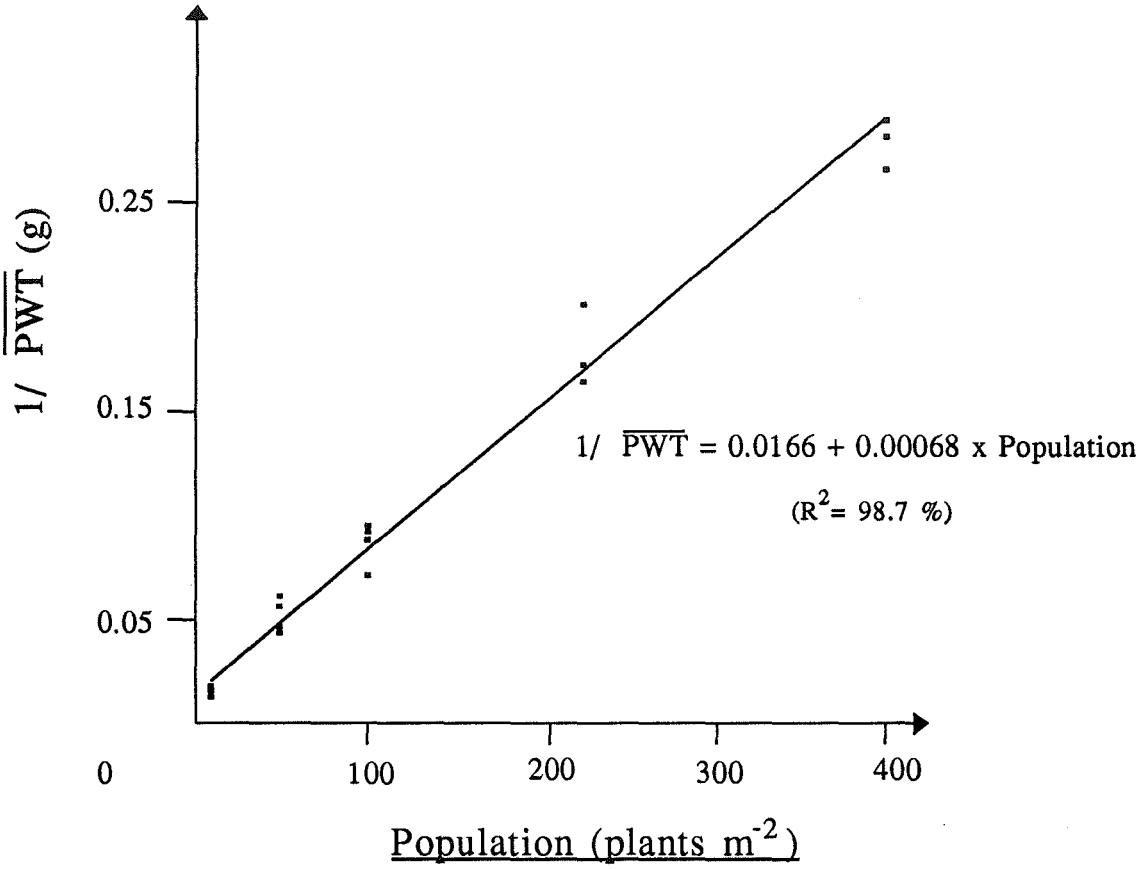
5.4.6 Effects of Population on PWT

5.4.6.1 Estimated maximum biological yield and mean PWT.

Analysis of the relationship between $\overline{PWT}$ and population gave highly significant linear relationships between 1/ $\overline{PWT}$ and population for all genotypes. All R^2 values were above 0.97. These results are illustrated for genotype CLU in Figure 5.3. For genotype CVN the intercept from the regression analysis was not significantly different from zero, so it was impossible to estimate the $\overline{PWT}$ (1/A) expected in a non-competitive environment. However, analysis of covariance indicated that the intercepts were similar for the other three genotypes. The values of 1/A for CLU, SVU, and SLU gave predicted $\overline{PWT}$ values of 60.2, 64.1 and 49.3 g $plant^{-1}$ respectively for non-competitive environments.

Analysis of the regression coefficients for slope indicated that the value of B from genotype CVN was significantly ($p<0.01$) higher than those from the other genotypes. Therefore, the estimated maximum biological yield (1/B) was lower for CVN (1245) than for CLU (1466), SVU (1427) or SLU (1513). These estimated maxima were higher than those observed at 400 plants m^{-2} (Figure 5.2) which implies that the biological yield produced at this highest population was below the environmental maximum.

Figure 5.3: Relationship between the inverse of mean plant weight and plant population for crops from genotype CLU, grown in the 1989/90 experiment.



5.4.6.2 Competition index. No significant (p=0.269) replicate effect was found for $\overline{PWT}$ so the PWT at 9 plants m^{-2} was used for the calculation of competition indices (Equation 5.5). For these spaced plants the dry weights of the largest plants were about double those of the mean plants, which resulted in competition indices of 176 to 201 (Table 5.7). At populations above 49 plants m^{-2} the competition indices for genotypes CVN and SVU were generally significantly lower than those from CLU and SLU (Table 5.7). For example, at 400 plants m^{-2} the competition indices from genotypes CVN (11.7) and SVU (12.3) were lower ($p<0.01$) than those from CLU (15.2) and SLU (15.4). There was also at least a 10 fold range in the PWT values at all populations. For example, for the spaced plants in replicate 1 of genotype CVN, the lowest PWT was 9.3 g and the largest was 136.6 g.

Table 5.7: Competition indices for field pea genotypes sown at five populations in the 1989/90 experiment. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different.

	Competition indices				
	Population (plants m^{-2})				
Genotype	9	49	100	225	400
CVN	187_a	62.3_a	36.0_b	17.4_b	11.7_b
CLU	182_a	64.7_a	38.4_{ab}	23.2_a	15.2_a
SVU	176_a	51.4_b	31.2_b	16.5_b	12.3_b
SLU	201_a	64.4_a	44.4_a	22.9_a	15.4_a
(SEM)	11.1	2.37	2.29	1.61	0.69

5.4.7 Yield Components

5.4.7.1 Pods per plant. The number of pods per plant decreased from an average of 31 at 9 plants m^{-2} to 2.2 at 400 plants m^{-2} (Table 5.8). At 9 plants m^{-2} genotype SVU averaged 10 pods $plant^{-1}$ more than the other genotypes ($p<0.01$), but at 49 and 100 plants m^{-2} there were no differences among genotypes ($p=0.37$). At 225 plants m^{-2} genotype CVN averaged fewer ($p<0.01$) pods per plant than CLU and SLU, and at 400 plants m^{-2} genotype CVN had fewer pods per plant than the other three genotypes.

5.4.7.2 Peas per pod. The mean number of peas per pod varied significantly among genotypes, but only decreased substantially at the two highest populations (Table 5.8). The conventional genotypes (CVN and CLU) had significantly ($p<0.01$) more peas per pod than the semi-leafless genotypes (SVU and SLU) at all populations.

5.4.7.3 1000 seed weight. The 1000 sw values were significantly ($p<0.01$) different among all genotypes. The 1000 sw of genotype SLU averaged 288 g compared with 265 g for SVU, 239 g for CVN and 214 g for CLU. The range of 1000 sw across populations was about 20 g for each genotype, with a highest standard error of 6.4 g.

5.4.8 Genotype by Environment Interaction

A summary of results from the split-plot analysis for seed yield, PHI and the yield components is presented in Table 5.9. The calculations of the sources of variation are based on a pre-requisite of a significant GXE term from the ANOVA for the split-plot analysis.

For seed yield the full ANOVA table is presented as an example to clarify the tests of significance for the split-plot analysis (Table 5.10). For seed yield, neither replicate nor

Table 5.8: Mean numbers of pods per plant and peas per pod for genotypes sown at five populations in the 1989/90 experiment. †Environmental means were used as the independent variable for analyses of stability. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different.

	Pods per plant				
	Population (plants m^{-2})				
Genotype	9	49	100	225	400
CVN	28.1_b	8.75_a	5.46_a	2.57_b	1.86_c
CLU	29.2_b	8.79_a	5.24_a	3.24_a	2.40_a
SVU	38.0_a	10.23_a	5.98_a	2.92_{ab}	2.11_b
SLU	28.1_b	8.89_a	5.96_a	3.22_a	2.28_a
(SEM)	1.97	0.610	0.361	0.132	0.071
†Environmental mean	30.9	9.16	5.66	2.99	2.16
Genotype	Peas per pod				
CVN	5.41_b	5.55_a	5.36_a	4.78_a	3.72_a
CLU	6.19_a	5.80_a	5.80_a	4.67_a	3.94_a
SVU	3.90_d	4.09_b	4.06_b	3.67_b	3.20_b
SLU	4.60_c	4.00_b	3.90_b	3.24_c	3.04_b
(SEM)	0.100	0.107	0.186	0.111	0.103
†Environmental mean	5.03	4.86	4.78	4.09	3.48

genotype effects were significant but the GXE and population effects were significant. From this ANOVA the expected mean square for genotypic variance (σ_g^2) was calculated (Section 5.3.2; Table 5.4) as a negative value and was therefore considered to be zero. Consequently the broad sense heritability was also estimated as zero and the GXE effect relative to genotype was estimated as infinity (Section 5.3.2; Table 5.9). These results indicate that direct selection for seed yield would not be feasible for these environments and genotypes.

Similar analyses of variance were performed for PHI and the yield components, and in each case significant GXE interactions were found. This indicates that the genotypic effects were dependent on plant population.

Table 5.9: Relative contribution of different sources of variance and broad sense heritability estimates (h^2bs). Results are for seed yield, plant harvest index and components of yield for field peas grown in the 1989/90 plant population experiment.

Source of variation	Seed yield per unit area	PHI	Pods per unit area	Peas per pod	1000 sw
$Genotype_{(a)}$	0	14.9 (L)	1.9 (L)	152.0 (H)	1309.1 (H)
$G \times E_{(a)}$	4.2	14.9 (L)	6.5 (L)	19.9 (L)	58.9 (M)
$G \times E_{(b)}$	∞ (H)	97.7 (H)	346.4(H)	13.0 (L)	4.5 (L)
h^2bs	0	0.097 (L)	0.016 (L)	0.525 (H)	0.821 (H)

KEY: *L = Low, M = Medium, H = High.*
(a) Environment effect set at 100
(b) Genotype effect set at 100

To distinguish between the suitability of characters as selection criteria the calculated relative contributions from different sources of variability were also classified as low, medium, or high (Table 5.9). For PHI the magnitude of genotypic effect was 14.9 % of the environmental effect and was classified as low. In contrast, the genotypic effect for 1000 sw was 13 times that of the environmental effect and was therefore classified as high.

Genotypic effects were low for pods per unit area and PHI, but the GXE interaction effect (relative to the genotype effect) was high and therefore comprised most of the variation in these characters. In contrast, genotypic effects and broad sense heritability estimates were high for peas per pod and 1000 sw. The magnitude of the GXE interaction effect (relative to the environmental effect) was only important for 1000 sw (Table 5.9).

5.4.9 Phenotypic Stability

5.4.9.1 Seed yield. Despite the significant interaction between genotype and environment for seed yield (Table 5.10), no significant differences were found between genotypes for the regression coefficients in the analysis of stability (Table 5.11). The coefficients ranged from 0.83 to 1.15 (Table 5.11; Column 3) and were all significantly different from zero (Table 5.11; Column 5). This indicates that the seed yield of all genotypes generally responded similarly to increasingly favourable environments. Furthermore, none of the genotypes had a coefficient that was significantly different from one (Table 5.11; Column 6), so they all exhibited a similar average stability across environments. This conflicts with the finding of a significant GXE (Table 5.10).

The significant interaction probably resulted from genotype CVN. The most favourable environment for it was E_4 (225 plants m^{-2}), not E_5 (400 plants m^{-2}) as found for the other genotypes. With such a range of environments, the overall trend of increased total seed yield with increased population may have masked this difference in the stability analysis.

However, the lower regression coefficient (0.83) and R^2 value (86.9 %) imply some deviation from the overall trend for genotype CVN. Thus, the direction of response for CVN was similar to the other genotypes, but not to the same extent.

Table 5.10: ANOVA for split-plot analysis of seed yield (m^{-2}). The replicate and genotype effects are tested against the replicate x genotype interaction ($F_{\alpha(3,9)}$). The environment and genotype x environment effects are tested against the error term ($F_{\alpha(4,48)}$ and $F_{\alpha(12,48)}$, respectively).

Source of variation	Degrees of freedom	Mean square	Expected mean square
Replicate (R)	3	1504.6	2.39
Genotype (G)	3	882.2	1.40
R X G	9	624.6	
Environment (E)	4	36486.4	123.93**
G X E	12	667.8	2.27*
Error	48	294.6	

*KEY: * and ** represent significance at the p<0.05 and 0.01 levels respectively.*

5.4.9.2 Pods per unit area. Genotypes CVN and CLU had average stability (b=1) for pods per unit area (Table 5.11) but genotype means were lower than environmental means for genotype CVN in all environments (Table 5.8). The ranking of environments (E_1-E_5) from lowest to highest for pods per unit area followed the increase in plant population (9 to 400 plants m^{-2}).

5.4.9.3 PHI. The stability analysis of PHI indicated a significant linear regression ($b \neq 0$) of genotype means over environmental means, and therefore that PHI increases as a linear function of improving environments, for the four genotypes. However, no difference from the regression slope (b=1) was found for genotypes CVN,

CLU and SVU, although the PHI means for genotype CLU were always higher than the environmental means (Table 5.11). The regression coefficient for SLU (b=0.69) was significantly lower than unity (b=1), suggesting a stable response across environments for this genotype (Table 5.11).

5.4.9.4 Peas per pod. The environmental ranking (E_1-E_5) for peas per pod from lowest to highest was the reverse of the plant population rankings (*i.e.* 400 to 9 plants m^{-2}). Peas per pod increased linearly ($p<0.01$) with increasingly favourable environments for individual plants ($b\neq0$) for all genotypes (Table 5.11). The regression coefficient indicated average stability (b=1) for the responses of both genotypes CVN and SLU. However, genotype means for CVN were always higher than environmental means, while for SLU means were always lower (Table 5.8). Genotype CLU produced an unstable response to environment (b>1), and its genotype means were always larger than the environmental means. In contrast, genotype SVU had a low regression coefficient (b=0.53), which indicates a low but stable response of peas per pod to the increasingly favourable environments.

5.4.9.5 1000 seed weight. Stability analysis for 1000 sw (Table 5.11) indicated that for genotypes CVN and SVU regressions were not significant (b=0) and had low R^2 values. However, all genotype means for CVN were lower than the environmental means while they were always higher for genotype SVU. For genotypes CLU and SLU the response was not significantly different from unity (b=1). However, genotype means for CLU were always lower than the environmental means. In contrast, they were always higher for SLU.

Table 5.11: Mean values and stability measures of seed yield, PHI and yield components. Results are for four field pea genotypes grown in five environments in 1989/90. $^{\dagger}R^2$ is the coefficient of determination.

Genotype	Mean	Regression coefficient	Standard error	b=0 t(df=3)p	b=1 t(df=3)f	$^{\dagger}R^2$ (%)
	(m^{-2})	Seed yield per unit area				
CVN	588	0.83	0.186	4.46	0.91	86.9
CLU	623	1.07	0.079	13.55**	0.89	98.4
SVU	573	0.95	0.030	31.17**	1.36	97.3
SLU	597	1.15	0.111	10.36**	1.74	99.7
	(%)	Plant harvest index				
CVN	55.1	1.52	0.181	8.39**	2.87	95.9
CLU	58.2	0.79	0.100	7.96**	2.15	95.5
SVU	55.1	0.97	0.145	6.73*	8.60*	99.2
SLU	56.0	0.69	0.036	19.10**	0.20	93.8
	(m^{-2})	Pods per unit area				
CVN	493	0.75	0.085	8.88**	2.91	96.3
CLU	574	1.24	0.106	11.63**	2.23	97.8
SVU	581	0.85	0.044	19.31**	3.44	99.2
SLU	573	1.16	0.032	35.25**	5.17	99.8
	(Number)	Peas per pod				
CVN	4.98	1.36	0.347	3.92*	1.02	83.6
CLU	5.28	1.46	0.058	25.10**	7.93*	99.5
SVU	3.80	0.53	0.127	4.21*	3.70*	85.5
SLU	3.74	0.93	0.203	4.60*	0.35	87.6
	(g)	1000 seed weight				
CVN	239	1.09	0.529	2.06	0.17	58.5
CLU	214	1.28	0.221	5.79*	1.27	91.8
SVU	265	0.48	0.430	1.12	1.21	29.4
SLU	288	1.20	0.334	3.61*	0.60	81.2

KEY: * *and* ** *represent significance at the 0.05 and 0.01 levels respectively.*

5.5 DISCUSSION

There were significant total seed yield differences between these morphologically distinct genotypes at the two highest populations. To determine ways for improving the seed yield of field peas it is important to identify the crop and plant characteristics associated with these yield differences. Ultimately seed yield may be improved by developing appropriate agronomic or breeding strategies from the plant characteristics which relate to high yields.

As a first step in identifying attributes associated with high seed yield, this discussion outlines the effects of changes in plant population on yield and harvest index and details the relationships between total seed yield and the yield components of field peas. The association between seed yield and each component is considered along with estimates of their heritability and stability to give an indication of their potential as selection criteria.

5.5.1 Agronomic Analysis

The relationships between plant population and yield exhibited the classical asymptotic response (Holliday, 1960a; 1960b). Both seed and biological yields almost doubled between 9 and 100 plants m^{-2} but there were no significant differences among the genotypes. From 100 to 400 plants m^{-2} each yield response flattened and seed yield differences ($p<0.01$) were found among the genotypes (Figure 5.1). Similar asymptotic relationships have previously been reported for field pea crops (Fallon and White, 1978; Heath *et al.*, 1991), indicating a stability of yield within seasons. However, Cousin *et al.* (1985) suggest yields are fairly constant from 50 to 200 plants m^{-2}, which is at odds with the lower yields from the 49 plants m^{-2} treatment in this study.

5.5.1.1 Yields, PWT and SWT. Differences in several of the variables used to describe crop yields followed a similar pattern to the seed and biological yield results, with significant differences observed only at the highest populations. Mean SWT and PWT values were similar among genotypes from 9 to 100 plants m^{-2}, but the mean SWT from genotype SVU was lower than CLU at 225 plants m^{-2} while at 400 plants m^{-2} CLU and SLU had higher mean SWT values than SVU and CVN had the lowest ($p<0.01$) mean SWT (Table 5.6).

The lower biological yield of genotype CVN at 400 plants m^{-2} was reflected in a lower mean PWT and a lower calculated maximum biological yield calculated for CVN (Section 5.4.6.1). Analysis of the competition indices also highlighted values from genotypes SVU and CVN as significantly lower than those from the other genotypes (Table 5.7). This indicates that under the same population treatment the interplant competition within these crops was greater than within crops from CLU and SLU. This association supports the general proposal of Ambrose and Hedley (1984) that competitive plant types may be less suitable as crop plants than low vigour types.

5.5.1.2 Yields, CHI and PHI. The differences in seed and biological yields were also reflected in the CHI and mean PHI values (Table 5.5). From 9 to 100 plants m^{-2} harvest index values were all within 2 % of their respective maximums for each genotype. However, at 225 and 400 plants m^{-2} genotype SVU produced a lower total seed yield, but a similar biological yield , to the other genotypes. This combination resulted in lower CHI and mean PHI values, and indicates a decreased proportion of the total biological yield was converted to seed yield for genotype SVU.

The significantly lower seed yield for CVN at 400 plants m^{-2} may have been caused by two mechanisms. The first was a decline in the proportion of biological yield converted to seed yield as population increased, but a second factor was its lower biological yield. This was also reflected in lower mean PWT values. To counter the lower biological

yield, and achieve a similar seed yield to the other genotypes, crops from genotype CVN would have had to convert a higher proportion of the dry matter to seed yield and consequently had higher CHI and mean PHI ~~high~~ values than the other genotypes. Possible explanations, based on biological characteristics, for the lower PHI and CHI values for CVN and SVU are presented in Chapter 7.

The differences in yield among genotypes were generally also reflected in the variables commonly used to describe yield; the lower yielding genotypes CVN and SVU had lower mean SWT, PWT, PHI and competition index values. Variability in PHI values resulting from either differences in SWT or PWT values has previously been mooted as a cause of low yielding genotypes (Ambrose and Hedley, 1984) and was central to initiating this study. To further investigate the causes of differences in seed yield and the variables used to describe yields, the frequency distributions for SWT, PWT and PHI will be examined in Chapter 6.

It should also be noted that when viewed strictly as a population experiment the population with the highest seed yield varied among genotypes. For genotype CVN, total seed yield was highest at 100 plants m^{-2} (Figure 5.1). The seed yield continued to increase from 100 to 400 plants m^{-2} for the other three genotypes, which indicates the maximum seed yield may be produced beyond the populations used in this experiment. However, the rate of increase for seed yield was low between 100 and 400 plants m^{-2} and this may actually cause an economic loss through increased seed costs needed to maximize the seed yield. At the usual commercially recommended population of 100 plants m^{-2} yields were similar for all genotypes (Figure 5.1).

The remainder of this chapter concentrates on the components of seed yield produced by genotypes at the various plant populations. The aim is to determine the relationship between seed yield and each component and consequently to examine the suitability of each component as a selection criterion for yield improvement.

5.5.2 Yield Components and Seed Yield

The yield components and morphology results at 9 plants m^{-2} highlighted contrasting attributes of the genotypes in this study. This lowest population was intended to minimize interplant competition, and therefore to approximate the spaced plant arrangement used for selection purposes in the early generations of pea breeding programmes. Although selection from spaced plants primarily screens lines for agronomic attributes and disease resistance, another objective is to identify genotypes with high yield potential.

Given the lack of significant yield differences between these genotypes at 9 plants m^{-2} the breeder is faced with a dilemma of separating these genotypes for yield potential using criteria other than their actual yield. For example, it is feasible that genotype CLU could be selected for its higher ($p<0.01$) number of peas per pod (Table 5.8), SVU for its larger number of pods per plant (Table 5.8), and SLU for the higher 1000 sw ($p<0.01$). The question is whether any of these attributes is relevant for improving yield potential at higher populations.

5.5.2.1 Pods per plant. To investigate the consequences of discriminating between genotypes on the basis of yield components, it is necessary to examine the relative importance of each component with increased competition. The consequences were exemplified by the changes in number of pods per plant with increasing populations. At 9 plants m^{-2} genotype SVU averaged 10 pods per plant ($p<0.01$) more than the other genotypes (Table 5.8), and in a breeding programme would clearly be noted for this characteristic. However, at the typical commercial population of 100 plants m^{-2} there were no significant ($p=0.122$) differences in pods per plant among genotypes. Thus, selection of genotype SVU for its superior number of pods at 9 plants m^{-2} did not translate to superior performance for this component, or for superior seed yield, at a commercial plant population.

Furthermore, the significantly lower number of pods per plant for genotype CVN at the highest population could be considered responsible for its lower seed yield. Plant breeders are generally not able to compare the yield performance of genotypes at several populations. Taken in isolation, the results at either 9 or 400 plants m^{-2} could be interpreted as highlighting the number of pods per plant as the critical yield component. Clearly it would be simplistic to conclude that this component could be used as a primary criterion for selection in a breeding programme. As shown earlier for genotype SVU, selection of plants with a high number of pods per plant at a low population could have little or no bearing on the number of pods per plant at higher populations.

In addition, both CVN and CLU were selected from parents with double or triple podding as a favourable attribute (Table 3.1). However, they did not show an advantage in pod numbers at any population, and no triple podding was observed at any node on any of the 7 456 plants harvested.

5.5.2.2 Peas per pod. Similar contradictions would occur if peas per pod was used as a selection criterion. At 9 plants m^{-2}, where no seed yield differences were observed, the number of peas per pod was significantly different between genotypes (Table 5.8). In contrast, at 400 plants m^{-2}, genotypes CLU and SLU produced similar numbers of peas per pod to genotypes CVN and SVU respectively, but had significantly higher seed yields.

5.5.2.3 1000 seed weight. Population changes had little effect on 1000 sw although differences ($p<0.01$) between genotypes were found at each population (Section 5.4.3). Genotype CLU, which achieved the highest seed yield, had the lowest 1000 sw (214 g) at all populations, while SLU produced a similar seed yield but had the highest 1000 sw (288 g). From these contrasting results it appears that genotypes with either the largest or lowest 1000 sw could be associated with high seed yield, so discrimination between these genotypes on the basis of 1000 sw would be impossible.

5.5.3 Genotype by Environment Interaction

The GXE analysis, broad sense heritability estimates and stability analysis offer some insight into the reasons for the poor relationships between individual yield components and seed yield for these genotypes.

5.5.3.1 Pods per unit area and PHI. A large GXE interaction (relative to the genotype effect) indicated that the plant population changes were the major cause of variability between genotypes for pods per unit area and PHI (Tables 5.10). These characteristics also showed low genotypic effects and low broad sense heritability estimates (Tables 5.8). This indicates that neither of these variables could be used to directly select for improved seed yield. This result supports the conclusion by Jermyn (1976) that harvest index is valueless as a selection criteria for direct yield improvement in field peas. Some yield improvement may be possible by selecting for stability of PHI across environments. Variation between individual plants within each crop will therefore be examined in Chapter 7 to determine if other characteristics related to PHI could be utilized as selection criteria.

The results for pods per unit area and PHI were similar to those reported for a separate germplasm pool by Samad (1988), who suggested that selection for stability of these characteristics within genotypes was essential. Assuming stability of pods per unit area or PHI are favourable attributes for a genotype, some discrimination between the four genotypes can be made. In particular, for pods per unit area, genotype SVU showed a stable response to favourable environments with genotypic means higher than each environmental mean. Genotype CLU showed a similar response for PHI (Table 5.5). In addition, genotype SLU also showed a stable response across populations for PHI (Table 5.11).

The stability of PHI results for genotypes CLU and SLU is further support for the proposal that high seed yield values may be associated with plant types that produce high stable PHIs. In contrast, the regression coefficient for CVN (Table 5.11) indicates an increase in PHI variability as environments changed.

5.5.3.2 Peas per pod and 1000 sw. Peas per pod and 1000 sw both showed high broad sense heritability estimates and a high genotypic effect (Table 5.9). Selection for these traits may therefore lead to yield improvement if they are stable and correlated with yield. Samad (1988) calculated a genotypic effect for peas per pod which was only 15 % of that found in this study, and also reported a broad sense heritability estimate of only 0.19 compared with 0.53 reported in this study. These conflicting results suggest that the heritability of peas per pod may be dependent on the initial germplasm pool selected and on the environment of testing. These anomalies between results cast doubts on the general usefulness of peas per pod as a stable yield indicator for field peas.

The 1000 sw results were similar to those presented by Samad (1988). The high broad sense heritability estimate of 1000 sw implies that further investigation into narrow sense heritability may be worthwhile. However, the highly variable R^2 values for 1000 sw (Table 5.11) indicate low consistency in the effect of environment on this component. Selection for 1000 sw would therefore be confounded by the environment of testing. In addition, Samad (1988) demonstrated a reversal of the correlation with yield and path coefficients between his diallel and GXE interaction trials. He concluded that 1000 sw would not be a reliable character to select for its association with improved yield because of this instability.

5.5.3.3 Yield components as selection criteria. Interpretation of the yield components, GXE and broad sense heritability estimate results have highlighted differences among genotypes and between plant populations in this study. However, none of these yield components could be identified to assist breeders improve yield and yield

stability of field peas. Significant differences in yield components were observed when seed yield differed at 225 and 400 plants m^{-2}. However, associating these differences to individual components and extrapolating back to performance at lower populations would be misleading. Yield components were limited in their ability to provide selection criteria for selection of the higher yielding genotypes.

5.5.3.4 Plasticity of yield components. The plasticity of yield components for field peas was highlighted by a comparison of stability analysis results from peas per pod and pods per unit area. The ranking of environments from least to most favourable was in reverse order for the two components. Furthermore, while genotype CVN produced a lower than average number of pods per unit area in all environments it also had a higher than average number of peas per pod in all environments. This mutual compensation of seed yield components is common for many crops (Adams, 1967; Grafton *et al.*, 1988; Pilbeam *et al.*, 1991) and suggests that manipulation of environmental factors to favour one component is likely to result in a compensatory decrease in the other yield components, with a relatively small net effect (Wilson, 1987).

Plant selections based on the number of pods per plant, number of peas per pod, or 1000 sw would all have resulted in a different genotype being selected from this experiment. The genotype chosen would also depend on the population at which the selections were made. At 100 plants m^{-2}, a typical commercial and yield trial population, these four genotypes could not be discriminated between on the basis of either total seed or biological yield.

5.6 CONCLUSIONS

In this experiment genotypes CLU and SLU produced a significantly higher seed yield than genotypes CVN and SVU at the highest populations. Significant differences in mean PHI and CHI occurred between the genotypes at the same populations. These differences reflected a failure of genotypes to convert the same proportion of their dry

matter to seed at higher populations. However, analyses of GXE interactions and broad sense heritability estimates showed direct selection for harvest index would not be feasible. However, genotypes CLU and SLU did show greater stability or had higher genotypic means than CVN and SVU for PHI across populations.

Further analyses indicated none of the yield components of field pea crops could be used to consistently discriminate between these genotypes at all populations. Consequently none of the yield components could be used as a selection criterion where its selection at one population could be expected to translate to superior performance at another. The second main assumption of this study (Section 1.2) was therefore fulfilled.

The agronomic and yield component analyses have provided a comprehensive summary of the effects of changes in plant populations on the yield of these four genotypes. However, they have not offered a method for discriminating between these genotypes nor a basis for explaining the physiological causes of these differences.

Analyses in Chapter 6 will use the data from this trial to test the PAM proposed in Chapter 4. The aim is to describe the effects of plant population in terms of the model components. Ultimately the aim to discriminate between genotypes for seed yield using plant characteristics associated with differences in the components of the PAM (Chapter 8).

CHAPTER SIX

VALIDATION OF THE PAM MODEL

6.1 INTRODUCTION

In Chapter 5, the effects of changes in plant population on the yield and yield components of four morphologically distinct field pea genotypes were investigated. Results indicated that the yield components could not be used consistently to discriminate between these genotypes or as selection criteria to improve seed yields. However, the two genotypes that produced the lowest seed yields (CVN and SVU) also had either the lowest mean SWT, PWT or PHI values. This result was consistent with the first main assumption of this thesis (Section 1.2), *viz.* that differences in seed yield between crops can be associated with differences in frequency distributions of SWT, PWT and PHI (Ambrose and Hedley, 1984).

In Chapter 4, relationships between SWT, PWT and PHI distributions were formalized into an empirical PAM. This PAM was proposed as a tool for investigating field pea crops. The model was based on a principal axis and an ellipse used to represent the relationship between SWT and PWT. The PAM was located within a set of defined boundary conditions (Section 4.4). Simulations were performed to examine the effects of changes in the mean and SD of SWT and PWT frequency distributions on the principal axis and ellipse. These simulations were also used to predict the changes in PHI values resulting from the changes in SWT and PWT.

A result of these simulations was the finding that when the SD of SWT and PWT change in similar proportions, the slope of the principal axis remains constant. The SWT axis

intercept and location of the ellipse are then dependent only on the mean coordinate ($\overline{PWT}$, $\overline{SWT}$). The dimensions of the ellipse (indicated by the internal area, projected lengths on both axes, and the axes ratio) were influenced by the scatter of points around the line and the magnitude of change in the SD values.

A further finding was that when changes in the SD of SWT and PWT were not equal, the principal axis rotated, the ellipse either elongated or contracted and the axes ratio changed. The responses of the principal axis and ellipse, and therefore the PHI, were predictable provided the data set remained within the defined boundaries. When some of the SWT and PWT values from a simulation were located outside a boundary, the components of the PAM were modified.

In this chapter the applicability of the PAM is tested using data from the 1989/90 population experiment as a validation set. The plant populations were chosen to represent a range of environments from spaced plants at 9 plants m^{-2}, up to highly competitive environments (225 and 400 plants m^{-2}) where substantial interplant competition was expected. The initial objective of this chapter is to determine whether the linear relationship between SWT and PWT remains under these varying agronomic conditions.

The components of the PAM are then related to changes in the frequency distributions of the SWT and PWT values caused by the changes in plant populations. The objective is to determine whether the assumptions of, and conclusions from, the simulation analyses of the PAM (Chapter 4) were valid when data sets with non-normal distributions were analyzed. It should then be possible to describe the yield expectations of crops on the basis of their frequency distribution values. The final objective is to compare the observed effects of population and genotype on the PHI values of plants with those predicted from the equivalent simulated changes in the model components, from the theoretical analyses in Chapter 4.

The experimental details and data analyses of this chapter are summarized in Section 6.2 with results presented in Section 6.3. The discussion focuses on validating the assumptions of the PAM by examining the relationship between SWT and PWT and the frequency distributions of SWT, PWT and PHI. Discrepancies between the observed and predicted responses of the components of the PAM are also discussed.

6.2 MATERIALS AND METHODS

6.2.1 Experimental Details

Details of the experimental design, genotype selection, site, soil preparation, plot sizes, plant numbers, crop husbandry and measurements taken were described in Chapter 5 (Section 5.2).

6.2.2 Data Analysis

6.2.2.1 Regression analyses. Least squares regression analysis of SWT against PWT was performed with the pooled data from the four replicates, but separately for each population, using the '*SAS*' statistical package (SAS Institute, 1990) and the '*PROC GLM*' procedure. Covariance analysis (Snedecor and Cochran, 1980) was used to compare the gradients and intercepts at each population. Where significant differences were found between regression coefficients, Tukey's honestly significant difference tests were used to quantify the separation (Zar, 1984).

A second series of regression and covariance analyses was performed after the data set had been adjusted for the degree of branching. This adjustment involved dividing the SWT and PWT values of each plant by its total number of branches.

6.2.2.2 Branching analysis. Chi-square analysis was used to compare the number of branched plants and the degree of branching for each genotype, at each population. To overcome the differences in plant numbers between populations, the results are presented on a percentage basis. Plants were classified for their level of branching as: none (main stem only), low (main stem plus one or two branches), medium (main stem plus three or four branches) or high (main stem plus five or more branches).

6.2.2.3 Frequency distributions. The frequency distributions for SWT, PWT and PHI from each of the 80 plots were analyzed for normality, skewness (g_1), and kurtosis (g_2) using the '*SAS*' statistical package and the procedure '*PROC UNIVARIATE*' (SAS Institute, 1990). This procedure also generated the SD and CV values. An ANOVA based on the split-plot design (Section 5.3.2; Table 5.9) was used to investigate differences between values of g_1 and g_2. A lack of any theoretical basis for assuming these estimates (g_1 and g_2) were normally distributed, and insufficient data points to test for normality meant that the reliability of mean separation tests was unknown (B.G. Love, pers. comm.) and the tests were not performed. Standard errors of the mean values of g_1 and g_2 are reported.

Critical values from the Students 't' distribution were used to determine whether values of g_1 and g_2 were significantly different from zero, and therefore the significance of skewness or kurtosis. The SD values were compared among genotypes at each population (Section 5.3.1) to ensure the assumption of equal variances was met. The CV values provide a useful, dimensionless parameter for comparisons between populations when the SD values vary with the mean (Sokal and Rohlf, 1981) as was observed in this study.

A second analysis of normality, skewness and kurtosis was performed for SWT, PWT and PHI distributions after the plant data had been adjusted for branching. The variables measured were defined as SWT per branch (SWT_b), PWT per branch (PWT_b), and PHI per branch (PHI_b).

6.2.2.4 Analyses based on the PAM. Data was also analyzed using the principal axis techniques developed in Chapter 4 to calculate the principal axis and ellipse for each treatment. The axes ratio and projected lengths on both axes are used to compare the ellipses among genotypes at each population.

6.3 RESULTS

6.3.1 Branching Analysis

At the lowest population, the number of branches per plant ranged between one, (just the main stem) and 12. Plants with no branches were grouped with the 'low' level of branching (Section 6.2.2.2) to maintain sufficient counts in each cell for Chi-square analyses. The hypothesis tested was that the degree of branching was equal among genotypes at each population. Genotypes CVN and CLU produced more ($p<0.01$) highly branched plants than expected, while genotype SLU produced greater numbers of plants with a low level of branching and fewer ($p<0.01$) highly branched plants than expected (Table 6.1).

Branching was suppressed as population increased. At 49 plants m^{-2}, up to 3 branches per plant were observed for approximately 1 % of each genotype. About 75 % of the conventional plants (CVN and CLU) produced one or two branches compared with 10.4 and 5.5 % of the SVU and SLU plants respectively (Table 6.1). A further breakdown of the low-branching plants at 49 plants m^{-2} showed that less than 1 % of the semi-leafless plants had two branches compared to 20.6 % for CVN and 12.3 % for CLU. At 100 plants m^{-2} all plants were either non-branched or had a low degree of branching. Both conventional genotypes again produced more branched plants than expected, while the semi-leafless genotypes produced fewer (less than 2 %) branched plants (Table 6.1).

Over 1500 plants were sampled at both 225 and 400 plants m^{-2}, and only five of these plants had produced one branch.

Table 6.1: Degree of branching (% of plants) for field pea plants harvested from the 1989/90 plant population experiment. Of the plants harvested at 225 and 400 plants m^{-2}, 99.7 % produced only a main stem.

Population (plants m^{-2})	Genotype	Branching categories (number of branches)			
		Main stem only	Low (1-2)	Medium (3-4)	High (>5)
9	CVN	0.9	17.6	45.2	36.2^{+}
	CLU	0.5	19.4	41.3	38.8^{+}
	SVU	3.0	13.9	56.4	26.7
	SLU	7.8	36.5^{+}	50.2	5.5^{-}
49	CVN	20.6^{-}	78.0^{+}	1.3	0
	CLU	26.0^{-}	73.5^{+}	0.5	0
	SVU	88.5^{+}	10.4^{-}	1.1	0
	SLU	94.2^{+}	5.5^{-}	0.2	0
100	CVN	51.3^{-}	48.7	0	0
	CLU	70.7	29.3^{+}	0	0
	SVU	98.2^{+}	1.8^{-}	0	0
	SLU	99.7^{+}	0.3^{-}	0	0

KEY: $^{+}$Higher cell count than expected. $^{-}$Lower cell count than expected.

6.3.2 Regression Analyses

6.3.2.1 Before adjustment for branching. Regression analyses of SWT against PWT for the 20 treatment combinations were linear, of the form:

$$SWT = a + b \times PWT,$$

with R^2 values between 93.8 and 98.8 % (Table 6.2).

Covariance analysis indicated significant differences among the gradients of genotypes at each population. Regression lines from the genotypes were therefore not pooled at any population. The gradient from genotype CVN was consistently higher than that from SVU, and SVU had the lowest gradient at all populations except 9 plants m^{-2}. Differences in the gradients of the other genotypes were dependent upon population (Table 6.2).

The SWT axis intercepts for all 20 treatment combinations were significantly less than zero ($p<0.01$), with the exception of CLU at 49 plants m^{-2}. At 9 plants m^{-2} the negative intercepts were at least double those calculated for higher populations (Table 6.2). For example, the SWT axis intercept for genotype CVN was -1.91 at 9 plants m^{-2} but between -0.329 and -0.623 for populations from 49 to 400 plants m^{-2} (Table 6.2).

From the regression coefficients, MPW values were calculated (Section 3.3.2), which ranged from 2.34 to 4.70 g at 9 plants m^{-2}, and from 0.01 to 1.09 g for the other populations (Table 6.2).

Table 6.2: Regression values for analyses of SWT against PWT prior to the adjustment for branching. Results are for plants harvested from the 1989/90 plant population experiment. Pooled standard errors (SE) are presented for the coefficients. Coefficients within a population, with a letter subscript in common are not significantly ($p<0.05$) different. †Minimum plant weight.

Population (plants m^{-2})	Genotype	Intercept (g)	Gradient	Coefficient of determination (%)	†MPW (g)
9	CVN	-1.91_{ab}	0.618_{a}	98.3	3.09
	CLU	-3.00_{a}	0.639_{a}	97.8	4.70
	SVU	-1.38_{b}	0.603_{b}	97.8	2.42
	SLU	-1.46_{b}	0.589_{b}	98.5	2.34
	(SE)	0.442	0.0057		
49	CVN	-0.548_{ab}	0.627_{a}	97.7	0.87
	CLU	-0.008^{+}_{c}	0.615_{a}	98.8	0.01
	SVU	-0.204_{bc}	0.596_{b}	96.8	0.34
	SLU	-0.678_{a}	0.623_{a}	98.1	1.09
	(SE)	0.0903	0.0055		
100	CVN	-0.623_{a}	0.631_{a}	96.8	0.99
	CLU	-0.128_{b}	0.621_{a}	98.7	0.21
	SVU	-0.214_{b}	0.599_{b}	96.0	0.36
	SLU	-0.178_{b}	0.598_{b}	98.0	0.30
	(SE)	0.6001	0.0050		
225	CVN	-0.366_{a}	0.647_{a}	98.3	0.57
	CLU	-0.104_{b}	0.606_{b}	97.8	0.17
	SVU	-0.301_{a}	0.601_{b}	93.8	0.50
	SLU	-0.289_{a}	0.633_{a}	97.7	0.46
	(SE)	0.0318	0.0052		
400	CVN	-0.329_{a}	0.650_{a}	97.5	0.51
	CLU	-0.204_{b}	0.639_{a}	98.6	0.32
	SVU	-0.231_{b}	0.600_{b}	94.6	0.39
	SLU	-0.264_{ab}	0.634_{a}	97.5	0.42
	(SE)	0.0189	0.0054		

6.3.2.2 After adjustment for branching. A second series of regression analyses was performed for data from the 9, 49, and 100 plants m^{-2} treatments after the SWT and PWT data had been adjusted for branching (Section 6.2.1.3). The resulting regressions were also highly significant ($p<0.01$) with R^2 values between 97.0 and 99.1 % (Table 6.3). Covariance analyses again indicated genotype differences at each population so pooling of results for genotypes was not possible.

Table 6.3: Regression values from the analysis of SWT_b against PWT_b at the three lowest populations in the 1989/90 experiment. Values for 225 and 400 plants m^{-2} were the same as in Table 6.2. †Minimum branch weight. Coefficients within a population with letter subscripts in common are not significantly ($p<0.05$) different.

Population (plants m^{-2})	Genotype	Regression values			
		Intercept (g)	Gradient	Coefficient of determination (%)	†MBW (g)
9	CVN	-0.496_b	0.627_b	97.7	0.79
	CLU	-0.966_a	0.666_a	98.1	1.45
	SVU	-0.559_b	0.607_b	97.2	0.92
	SLU	-0.737_{ab}	0.620_b	97.6	1.19
	(SE)	0.1160	0.0073		
49	CVN	-0.326_b	0.632_a	98.5	0.52
	CLU	-0.098^+_c	0.625_a	99.1	0.16
	SVU	-0.198_{bc}	0.597_b	97.5	0.33
	SLU	-0.671_a	0.624_a	98.3	1.08
	(SE)	0.0689	0.0042		
100	CVN	-0.329_a	0.619_a	97.8	0.53
	CLU	-0.086^+_b	0.619_a	98.7	0.14
	SVU	-0.249_{ab}	0.602_b	97.0	0.41
	SLU	-0.173_{ab}	0.598_b	98.1	0.29
	(SE)	0.0478	0.0044		

KEY: †Value not significantly different from zero.

The SWT axis intercepts for all but CLU at 49 and 100 plants m^{-2} were less than zero ($p<0.01$) with calculated minimum branch weight (MBW) values from 0.14 to 1.45 g.

6.3.3 Frequency Distributions

6.3.3.1 Seed weight. Analysis of the SWT distributions indicated differences among genotypes and plant populations for skewness (g_1) and kurtosis (g_2).

Values of g_1 and g_2 for genotype CLU were higher than from other genotypes, and indicated distributions from CLU were positively skewed and leptokurtic (Table 6.4). Genotype SVU had the lowest g_1 value but, overall, values of g_1 and g_2 indicated SWT distributions for genotypes CVN, SVU, and SLU were normally distributed.

At 9 plants m^{-2} the SWT distributions were normally distributed, but they were leptokurtic from 49 to 400 plants m^{-2}. There was also a progressive increase in the degree of positive skewness (g_1) detected as population increased (Table 6.4).

The SD values for SWT were significantly different ($p<0.01$) between genotypes at 9 and 400 plants m^{-2} and were lowest for SVU at all populations (Table 6.5). Across populations, the SD fell from about 16 g at 9 plants m^{-2} to 1.1 g at 400 plants m^{-2}. In contrast, the CV values generally increased to be highest at 400 plants m^{-2} (Table 6.5).

6.3.3.2 Plant weight. The frequency distribution values for PWT followed the same pattern as those for SWT. Values of g_1 and g_2 were again highest for genotype CLU. Positive skewness was detected for CVN, CLU, and SLU and leptokurtosis was also indicated for CLU, SLU and SVU (Table 6.4).

The PWT values were normally distributed at 9 plants m^{-2}, but were both positively skewed and leptokurtic ($p<0.01$) from 100 to 400 plants m^{-2}.

The SD decreased across populations with significant differences between genotypes at 9 and 400 plants m^{-2} (Table 6.5). The CV values were similar from 9 to 100 plants m^{-2} but increased to be highest at 400 plants m^{-2}. The CV was lowest for SVU at each population.

Table 6.4: Skewness (g_1) and kurtosis (g_2) values for SWT, PWT, and PHI distributions before adjustment for branching. Values are for four genotypes and five populations in the 1989/90 experiment.

	Seed weight		Plant weight		Plant harvest index	
Genotype	g_1	g_2	g_1	g_2	g_1	g_2
CVN	0.27	0.08	0.28**	0.19	-2.34**	8.10**
CLU	0.56**	1.08**	0.71**	1.62**	-2.89**	13.80**
SVU	-0.07	0.29	0.04	0.48*	-2.83**	13.23**
SLU	0.31	0.26	0.40**	0.50*	-2.61**	10.53**
(SEM)	0.181	0.161	0.090	0.192	0.235	2.115
Population (plants m^{-2})						
9	-0.01	-0.23	-0.04	-0.23	-1.40**	3.92
49	0.13	0.68**	0.20	0.75**	-2.68**	13.06**
100	0.27	0.67**	0.42**	0.93**	-3.81**	21.07**
225	0.37	0.53**	0.53**	1.04**	-3.19**	13.56**
400	0.59*	0.49**	0.67**	0.99**	-2.23**	5.51**
(SEM)	0.202	0.180	0.100	0.216	0.262	2.361

*KEY: * and ** represent values significantly different from zero at the 0.05 and 0.01 levels.*

Table 6.5: Dispersion statistics for SWT, PWT and PHI distributions for field pea crops grown in the 1989/90 population experiment. †SD is the standard deviation and CV is the coefficient of variation. SD values with a letter subscript in common are not significanlty different within a population.

Population (plants m^{-2})	Genotype	SWT		PWT		PHI (%)	
		SD (g)	CV (%)	SD (g)	CV (%)	SD	CV
9	CVN	19.6_a	49.3	31.4_a	46.0	4.68_a	8.1
	CLU	16.8_{ab}	41.5	26.4_{ab}	39.0	4.75_a	8.2
	SVU	13.0_c	32.3	21.9_b	31.3	3.30_a	5.8
	SLU	14.1_{bc}	39.3	23.4_b	38.0	3.18_a	5.6
	(SEM)	0.68		1.03		0.372	
49	CVN	5.03_a	41.0	7.89_a	39.0	4.78_a	8.1
	CLU	4.88_a	41.0	7.81_a	40.3	3.65_a	6.0
	SVU	3.80_a	33.8	6.32_a	33.0	4.38_a	7.6
	SLU	4.01_a	36.8	6.44_a	34.0	4.40_a	7.6
	(SEM)	0.269		0.479		0.381	
100	CVN	2.95_a	42.5	4.71_a	38.8	6.45_a	11.4
	CLU	2.73_a	39.0	4.30_a	37.8	5.63_a	9.4
	SVU	2.25_a	34.3	3.75_a	31.5	5.00_a	8.7
	SLU	2.90_a	41.3	4.68_a	39.3	7.25_a	12.9
	(SEM)	0.131		0.212		0.586	
225	CVN	1.53_a	48.3	2.18_a	43.5	10.65_a	19.4
	CLU	1.70_a	51.0	2.70_a	49.0	8.08_a	14.2
	SVU	1.35_a	46.0	2.31_a	39.5	10.85_a	21.4
	SLU	1.68_a	52.8	2.68_a	48.3	11.85_a	21.6
	(SEM)	0.068		0.131		0.919	
400	CVN	1.00_b	61.8	1.72_{ab}	56.8	18.68_a	40.9
	CLU	1.30_a	63.3	2.03_a	57.8	12.45_a	23.2
	SVU	0.98_b	52.8	1.43_b	42.3	11.98_a	24.0
	SLU	1.22_a	59.0	1.89_a	51.5	13.35_a	25.8
	(SEM)	0.041		0.071		1.048	

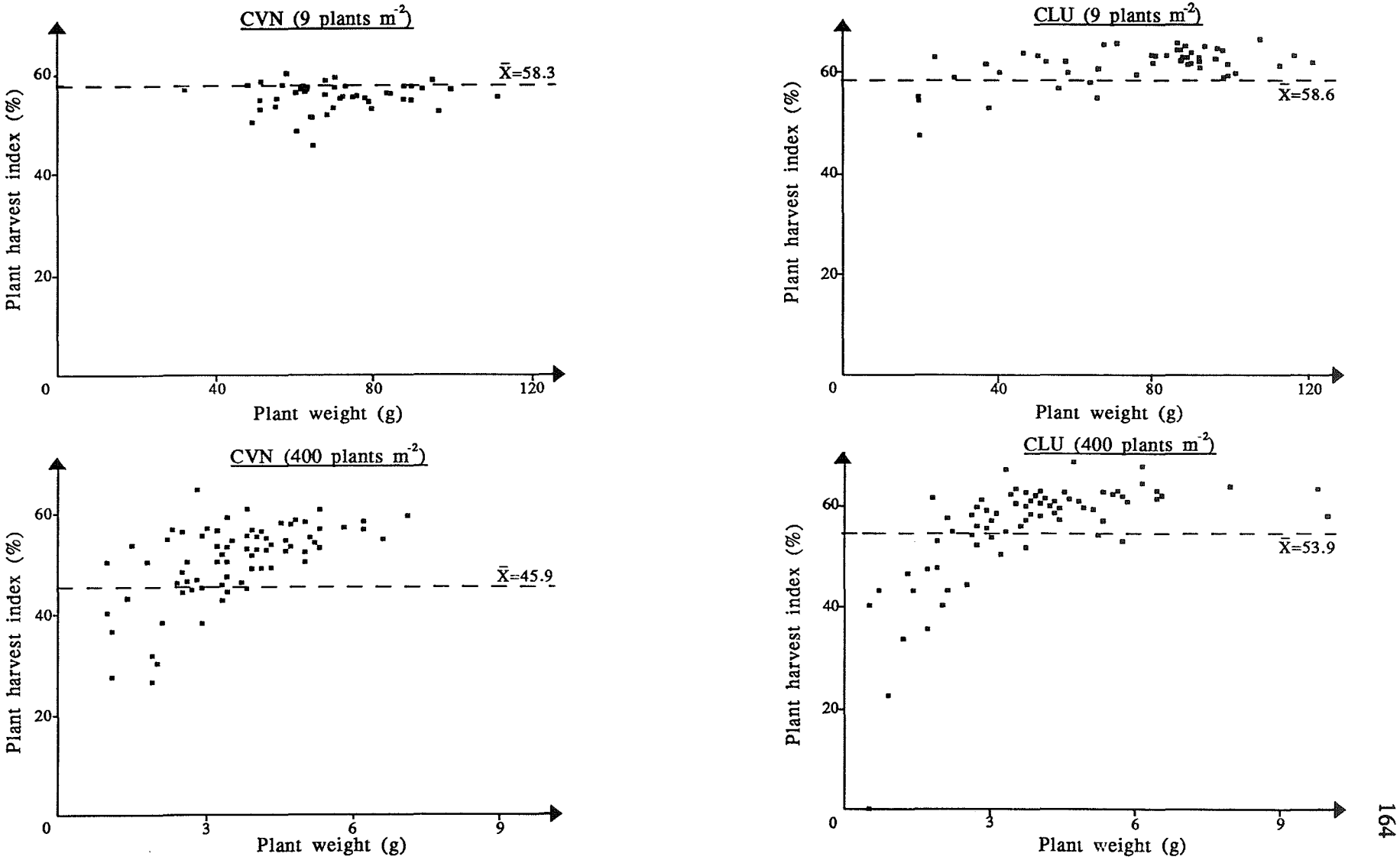
6.3.3.3 Plant harvest index. All genotypes and plant populations resulted in negatively skewed ($p<0.01$) PHI distributions (Table 6.4). Only the distributions from spaced plants were not also leptokurtic. The SD values for each genotype were about 5 % from 9 to 100 plants m^{-2} but increased to between 12 % (SVU) and 19 % (CVN) at 400 plants m^{-2} (Table 6.5). The CV values increased across populations from about 7 to 24 % for genotypes CLU, SVU, and SLU but the CV was 41 % for CVN at 400 plants m^{-2} (Table 6.5).

6.3.3.4 PHI versus PWT. The relationships between PHI and PWT were consistent with the results from the PHI distributions. At 9 plants m^{-2} the gradients of these relationships were not significantly different from zero (b=0) with values tightly grouped around the mean and median values. These relationships are illustrated by replicate one of genotypes CVN and CLU in Figure 6.1. The relationships do not reflect the asymptotic trend predicted in Chapter 4. However, at 400 plants m^{-2} an asymptotic trend was apparent with the effect greatest for genotype CVN (Figure 6.1).

6.3.3.4 Distributions of SWT_b, PWT_b and PHI_b. The mean SWT_b and PWT_b values differed significantly both among genotypes and populations. In general, the conventional genotypes (CVN and CLU) produced lower SWT_b and PWT_b values, and these values decreased as population increased (Table 6.6). No branching was observed at the two highest populations and the SWT_b and PWT_b values were therefore equal to the mean SWT and PWT values based on the whole plant data reported previously (Table 5.6).

Values of g_1 and g_2 indicated both the SWT_b and PWT_b distributions showed greater positive skewness and leptokurtosis than the whole plant data. For SWT_b, significant positive skewness was detected for genotypes CVN, CLU and SLU and the 49 to 400 plants m^{-2} populations (Table 6.6). All four genotypes and the 9 to 225 plants m^{-2} populations were also leptokurtic. For PWT_b, significant leptokurtosis and positive skewness was detected for all genotypes and populations.

Figure 6.1: Relationship between plant harvest index and plant weight. Data is from replicate 1 of genotypes CVN and CLU sown at 9 and 400 plants m^{-2} in the 1989/90 experiment.



The values for PHI_b were equal to those from the whole plant data. This result agreed with the arithmetic operation of dividing SWT and PWT by a common value, in this case the number of branches.

Table 6.6: Summary statistics of frequency distributions for SWT_b and PWT_b. Mean, skewness (g_1) and kurtosis (g_2) values are presented for plants harvested from the 1989/90 plant population experiment. Mean values with a letter subscript in common are not significantly ($p<0.05$) different within each section of the table.

Genotype	Seed weight			Plant weight		
	Mean (g)	g_1	g_2	Mean (g)	g_1	g_2
CVN	4.85_c	0.50^{**}	0.65^{**}	8.51_b	0.69^{**}	1.04^{**}
CLU	5.16_b	0.51^{**}	1.28^{**}	8.74_b	0.85^{**}	1.85^{**}
SVU	5.94_b	-0.12	0.61^{**}	10.79_a	0.28^{**}	0.83^{**}
SLU	6.53_a	0.33^{**}	0.50^{**}	11.28_a	0.52^{**}	0.78^{**}
(SEM)	0.189	0.090	0.206	0.344	0.101	0.309
Population (plants m^{-2})						
9	8.59_a	-0.01	-0.77^{**}	15.10_a	0.51^{**}	0.85^{*}
49	8.47_a	0.30^{**}	1.14^{**}	14.45_a	0.58^{**}	1.51^{**}
100	6.00_b	0.28^{*}	0.87^{**}	10.57_b	0.64^{**}	1.26^{**}
225	3.18_c	0.37^{**}	0.53_*	5.48_c	0.53^{**}	1.04^{**}
400	1.88_d	0.59^{*}	0.49	3.39_d	0.67^{**}	0.99^{**}
(SEM)	0.208	0.103	0.238	0.384	0.111	0.337

*KEY: * and ** represent values significantly different from zero at the 0.05 and 0.01 levels.*

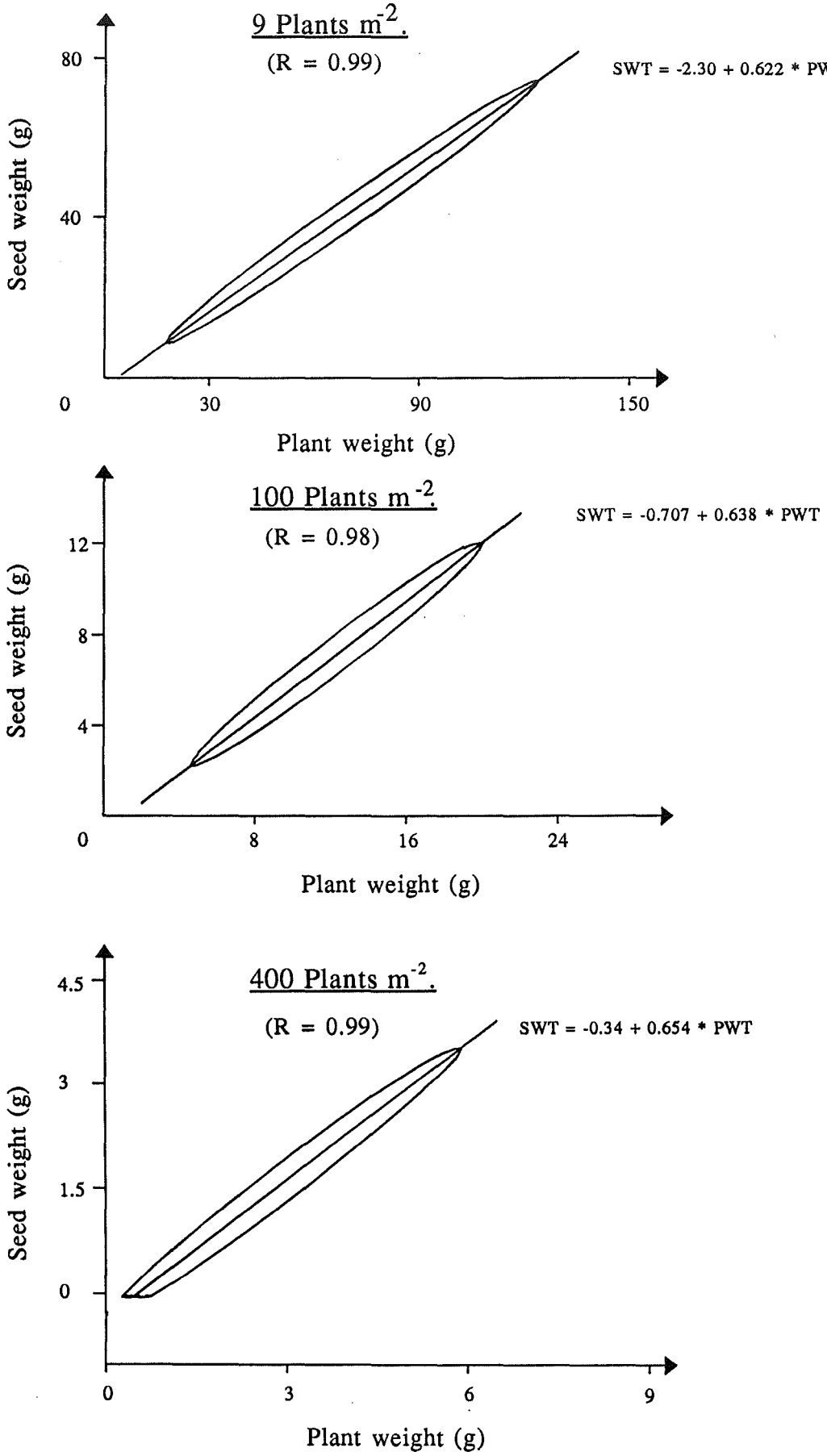
6.3.4 Analyses Using the PAM

The results from the principal axis analyses were similar for each genotype at each population. Results for genotype CVN at 9, 100 and 400 plants m^{-2} are presented to illustrate the main points.

6.3.4.1 Principal axis. The coefficients for SWT axis intercept were -2.30, -0.707 and -0.340 at 9, 100 and 400 plants m^{-2} with slopes of 0.622, 0.638 and 0.654 (Figure 6.2).

6.3.4.2 Ellipse. The correlation coefficients were 0.991, 0.984 and 0.987 at 9, 100 and 400 plants m^{-2}. These high values were reflected in the high axes ratios of 16.5, 12.2 and 13.4. The major influence of the increased plant populations was the decrease in the projected lengths. The projected length on the PWT axis at 9 plants m^{-2} was 104.9 g. There was a seven-fold decrease to 15.3 g at 100 plants m^{-2} and an 18 fold decrease to 5.8 g at 400 plants m^{-2}. The decreases of the projected lengths on the SWT axis were of a similar magnitude, down from 65.3 g at 9 plants m^{-2} to 9.7 and 3.8 g at 100 and 400 plants m^{-2} respectively (Figure 6.2).

Figure 6.2: Principal axis components from analyses of seed weight against plant weight of genotype CVN sown at 9, 100 and 400 plants m^{-2} in the 1989/90 experiment. R is the correlation coefficient.



6.4 DISCUSSION

This discussion focuses initially on the suitability of the linear relationship between SWT and PWT as the basis for the PAM. The effects of changes in plant population on the principal axis and ellipse are then described and related to changes in the SWT and PWT distributions. The implications for PHI values, of changes in the components of the PAM, are then discussed.

6.4.1 Relationship Between SWT and PWT

The regression relationships between SWT and PWT calculated from all 20 treatments were linear and highly significant with R^2 values above 93.8 %. This relationship was consistent, despite the contrasts in plant morphology and the 40-fold change in plant population. The consistency of this relationship supports its use as the basis of the PAM for examining field pea crops.

The implication from the high R^2 values, is that the coefficients for the principal axis would be similar whether least squares or principal axis regression techniques were used (Section 4.6). This assumption was supported by the comparison of coefficients from each method, as illustrated for CVN (Table 6.2; Figure 6.2). Attention is therefore focused on the coefficients produced rather than the method of calculation.

Differences in the regression coefficients for the principal axis were found among genotypes and populations. Thus, no one equation could be used to describe the relationship between SWT and PWT for field pea crops generally, nor for individual genotypes at all populations. By defining the position of the principal axis and ellipse at 9 plants m^{-2} as the control for each genotype, the effects of changes in plant population on the components of the PAM can then be assessed.

6.4.2 Effects of Plant Population on the Principal Axis

Differences in the coefficients among genotypes were generally less than those observed among populations (Table 6.2). The coefficients for slope varied by about 10 %, from 0.589 to 0.650 over the 20 treatments, but by less than 6 % within each genotype. In contrast, the SWT axis intercept at 9 plants m^{-2} was at least double that from other populations. Furthermore, the SWT axis intercept for all but one of the 20 treatments was negative. The consistent calculations of a negative SWT axis intercept supports the hypothesis of a MPW for these field pea genotypes and is consistent with previous analyses (Ambrose and Hedley, 1984; Chapter 3). The implications of this result are explored in Section 8.3.1.

The changes in the coefficients of the principal axes indicate that the increased plant populations resulted in a principal axis with a similar slope, but positioned to the left of the control for each genotype. The small, inconsistent changes in the gradients of these axes indicate that rotation of the axes was minimal and implies that the magnitude of changes in the SD values of the SWT and PWT distributions were the same within each crop (Simulations A-H; Section 4.3.2). This interpretation, based on the previous theoretical analyses (Chapter 4), was supported by the actual SD values for SWT and PWT, which declined approximately 20-fold for each genotype as populations increased from 9 to 400 plants m^{-2}.

The low SWT axis intercepts at 9 plants m^{-2} also indicate that the MPW was largest for the spaced plants. Possible reasons for this are discussed in Section 6.4.5.

6.4.3 Effects of Plant Population on the Ellipse

The second component of the PAM is the ellipse, which represents the distribution of data points around the principal axis. With R^2 values of at least 93.8 % (Table 6.2)

for the 20 treatments, the correlation coefficients were all above 0.97 and therefore substantially higher than those used for any of the simulations (R=0.71) in Chapter 4.

These high correlation coefficients indicate that the deviation around each axis was minimal, and that the ellipse calculated to contain 75 % of the data points (Section 4.3.1.2) had effectively collapsed onto each axis. The comparisons of the ellipses which follow therefore concentrate on how the changes in SWT and PWT distributions (resulting from the changes in population) affect the location and projected length of each ellipse.

The location of each ellipse can be interpolated from the mean SWT and PWT values presented in Chapter 5. Both of these values showed approximately a 20-fold decrease as population increased from 9 to 400 plants m^{-2}. This indicates that the mean coordinate ($\overline{PWT}$, $\overline{SWT}$) for the ellipse moved down the regression line, closer to the origin, as plant population increased. The values of g_1, g_2 and SD indicate that the structure of the SWT and PWT distributions was also affected by changes in plant population.

The degree of positive skewness for SWT and PWT distributions increased with population (Table 6.4). The distributions were normally distributed at 9 plants m^{-2} but positively skewed at 100 , 225 and 400 plants m^{-2} (Table 6.4). The CV values were similar from 9 to 100 plants m^{-2} but increased at the two highest populations (Table 6.5). The tendency for CV values for PWT to increase with plant population is consistent with previous studies (Edmeades and Daynard, 1979; Benjamin and Hardwick, 1986) and is considered to result from greater interplant competition for above-ground resources, particularly for light (Koyama and Kira, 1956; Weiner *et al.*, 1990).

Although the structure of SWT and PWT distributions varied across populations there was no indication that the axes ratio of the ellipses were affected. That is, the consistently high R^2 values (Tables 6.2 and 6.3) and the absence of outliers in all 20 treatments indicate that the relationship between SWT and PWT remained strong, with data points

located close to the principal axis, despite the presence of skewness and/or kurtosis. The 20-fold decrease in SD values as populations increased was also reflected in the ellipses. At 9 plants m^{-2} the ellipse for each genotype had the largest internal area and projected lengths on both axes (Figure 6.2). From 9 to 100 plants m^{-2} the reductions in SD values (Table 6.5) and mean PWT values (Table 5.6) were about six fold. This was consistent with the stable CV values for both SWT and PWT (Table 6.5). The reductions in the projected lengths and internal areas of the ellipses also reflected these reductions (Section 6.3.4.2).

In contrast, at the two highest populations the reduction in the projected lengths was less than that anticipated from the decreases in mean values (Table 5.6). Effectively, the SD values for SWT and PWT increased relative to the mean, which was also consistent with the increase in CV values (Table 6.5).

6.4.4 Summary of the Effects of Plant Population

The changes in plant population caused the values of SWT and PWT to vary, and resulted in significant differences in the frequency distributions of SWT and PWT values. Despite these variations, the data from each crop could be viewed in terms of the PAM proposed in Chapter 4.

The relationship between SWT and PWT was linear and strong across all treatments. In addition, the gradient for the principal axis of each genotype was similar across populations which resulted from the consistency in the reductions of SD values for the SWT and PWT distributions. The SWT axis intercepts from the spaced plants were the lowest and consequently the MPW calculated for each of the genotypes was highest at this population.

The major influence of the increases in plant population was the relocation of the ellipse down towards the origin. In addition, the internal area and projected lengths on both the SWT and PWT axes decreased. Thus, overall, the increases in plant population resulted in the location of a smaller ellipse (with a similar principal axis and axes ratio) closer to the SWT and PWT axis boundaries.

Several of the results from this data set highlight the robustness of the PAM. Firstly, the simulated data in Chapter 4 represented bivariate normal SWT and PWT distributions. In this chapter, significant skewness and kurtosis were detected which indicates the mean coordinates would not be centrally located (Section 4.4.2). Nevertheless, the data from these non-normal distributions were successfully described in terms of the components of the PAM. Secondly, the degree of branching differed between the conventional and semi-leafless genotypes, and among populations, but this did not appear to affect the descriptions of these crops in terms of the PAM.

6.4.5 Plant Harvest Index

The third aspect of testing the PAM is to examine the effects of the changes in the components of the PAM on the PHI values, and to compare these with the changes in PHI predicted in Section 4.5.

As the location of the ellipse approaches the PWT boundary the influence of the MPW was predicted to increase (Section 4.5), causing greater variability in the PHI values. The frequency distribution results for PHI in this experiment indicate that variability did increase as the plant population increased and the mean PWT decreased. The PHI distributions were all negatively skewed but as population increased the degree of kurtosis decreased and the CV values increased (Table 6.5).

The results for PHI indicate that at 9 plants m^{-2} each plant was achieving close to its genetic and physiological potential. The seed yield per plant was therefore at a maximum for this environment for each of the genotypes. With all plants achieving a high PHI, the expected asymptotic relationship between PHI and PWT (Section 4.5) did not occur (Figure 6.1). It follows, that the lack of a distinct asymptotic relationship can be explained by the range of PWT values for each crop. The results indicate that at populations below 400 plants m^{-2} the range of PWT values was beyond the initial linear phase of the asymptotic relationship and consequently variability in PHI values was low. Under different agronomic conditions, this linear phase may be located at higher PWT values and consequently plants of the same dry weight may produce varying PHI values. This hypothesis is explored in greater detail in Section 8.2.

The lack of variability in PHI values also indicates that the innate genetic variability for PHI proposed by Hedley and Ambrose (1984), was not apparent for these genotypes.

However, as the plant populations were increased the degree of interplant competition also increased and there was greater plant-to-plant variability in PHI values. The increased populations also resulted in a trend towards an asymptotic relationship and this was obvious for genotype CVN at 400 plants m^{-2}. At this population the majority of the plants from CVN retained high PHI values, but the lower PHI values could again be associated with the smaller plants in the population (Hedley and Ambrose, 1981; 1985; Chapter 3). Indeed, for both conventional genotypes, plants below about 4 g of dry weight tended to have the lowest PHI values. A further inference from the relationship between PHI and PWT is that at higher plant populations than those tested, PHI variability would increase due to the lower PWT values and increasing influence of the MPW. A more distinct asymptotic relationship would also be expected.

At 400 plants m^{-2} the SD and CV values for PHI were higher for CVN than the other genotypes. These differences indicate that the behaviour of plants in this treatment had been modified. Modification may have occurred due to the population of plants

approaching a biological boundary, as outlined by the boundary conditions of the PAM. In this situation, the simple 'line plus ellipse' model is altered and the boundary conditions must be considered to predict results. Specifically, the mean SWT and PWT values, and therefore the mean coordinate for CVN, was lower than for the other genotypes at 400 plants m^{-2}. This indicates that for CVN the ellipse was located closer to the PWT axis boundary than for the other genotypes and that the influence of the MPW on PHI values would be greatest for CVN. For SVU the position of the ellipse was similar to the high yielding genotypes (Table 6.2), but it had a lower gradient of the principal axis, which translates into a lower asymptote for the PHI values. In contrast, the lower MPW value for CLU was associated with higher mean PHI values and the higher seed yield. The implications for seed yield of these differences in PAM components are discussed further in Chapter 8.

6.4.6 Adjustment for Branching

The components of the PAM were used to describe the effects of changes in plant population. However, there appeared to be an anomaly with the lowest SWT axis intercepts and highest MPW values occurring at 9 plants m^{-2}. It was expected that interplant competition would be lowest at this population and therefore that the MPW requirement would be the smallest.

Leverage, whereby a few outlying points strongly influence fitting of the principal axis, seems unlikely to have caused the lower SWT axis intercepts in the spaced plant treatments. The regression analyses were based on a large number of data points (about 200 per genotype), the R^2 values were high, there were even spreads of points across the PWT ranges (indicated by the normal distributions of PWT), and there were no significant outliers.

These high MPW values may have resulted from the higher degree of branching of spaced plants. If each branch competed for resources in a similar manner to the individual plants at higher populations, then interplant competition would have been low but intraplant competition would have been high.

Support for this hypothesis, of high intraplant competition, is drawn from a comparison of the FD values before and after their adjustment for branching. At the whole-plant level, the lack of significant positive skewness at 9 plants m^{-2} suggests that interplant competition for above-ground resources was lowest at this population (Koyama and Kira, 1956; Weiner *et al.*, 1990), which is consistent with the competition indices calculated previously (Table 5.7). However, after the adjustment for branching, positive skewness was observed (Table 6.6) which suggests that intraplant competition occurred between branches on the same plant.

The mean SWT_b and PWT_b values for the conventional genotypes were lower than from the semi-leafless genotypes (Table 6.6) which reflects their higher degree of branching (Table 6.1) and, when coupled with their higher values of g_1 for PWT_b, implies that intraplant competition may have been greater in the conventional genotypes, than in the semi-leafless genotypes.

Thus, the inclusion of the widely spaced plant treatment to represent a non-competitive environment appears valid at the whole-plant level. However, results may be confounded for branched plants unless branches are the unit of measure. After adjusting the SWT and PWT values for branching (Section 6.2.2.2), regression analyses were recalculated for the 9 to 100 plants m^{-2} treatments. This second analysis reduced the overall range of SWT axis intercepts to between -0.496 and -0.966 for genotypes CVN and CLU respectively (Table 6.3). The coefficients for slope of the principal axis were similar to those found prior to the adjustment (Tables 6.2 and 6.3).

The calculated MBWs at 9 plants m^{-2} were still approximately double the MBW values at the higher populations. The extrapolation of the regression lines beyond the observed data at 9 plants m^{-2} could have led to uncertainties in the MPW calculations. Alternatively, the differences between MBW values at low and high populations may reflect a higher MBW requirement for heavily branched plants. That is, the efficiency of partitioning dry matter to seed may be lower for branches then the main stem. Weiner *et al.* (1990) suggested that this phenomenon occurs when a spaced plant is unable to expand its resource base in proportion to the increasing amounts of plant tissue, because some costs increase disproportionately. They suggested that biochemical constraints limit the size that upright plants can achieve without allocating an increasing proportion of their energy to structural tissue. This concept of increasing costs associated with structural development is implicit in the uniculm wheat ideotype proposed by Donald (1968).

It was observed that the development of branches in these indeterminate field peas was a continuous process throughout the season. This meant that both reproductive and vegetative branches were present at harvest. Indeed, observations at harvest indicated that interbranch variation for harvest index was high, with some branches barren while others produced seed in proportion to their branch weight. Thus, the variation in PHI for each branch would manifest as a lower PHI_b than predicted from their PWT.

Further indirect evidence to support the hypothesis of increasing costs with multi-stemmed plants was apparent in the mean PHI results presented in Chapter 5 (Table 5.5). An assumption related to the calculation of MPW values was that the slope of the regression line would become an asymptote for mean PHI values as mean PWT increased, due to the decrease in the influence of the MPW. From 400 plants m^{-2} down to 49 plants m^{-2} this assumption held, with an increase in mean PHI observed. However, there was a fall in mean PHI between 49 and 9 plants m^{-2}, for all genotypes. This decline in PHI may have been caused by lower partitioning efficiency of dry matter to seed due to the heavily branched nature of these plants.

6.5 CONCLUSIONS

In this chapter the PAM proposed in Chapter 4, was tested to determine whether the effects of changes in plant population on SWT, PWT and PHI could be described in terms of its components. This objective was achieved, with the effects of plant population summarized in terms of their effect on the principal axes and ellipse which describe the relationship between SWT and PWT. This relationship was consistently strong and linear, with similar gradients for each genotype across populations, even though significant differences in the structure of SWT and PWT distributions were evident. The negative SWT axis intercepts confirmed the hypothesis of a MPW for field peas. For heavily branched plants this may be more accurately defined as a minimum branch weight. The strength of the relationship between SWT and PWT over a wide range of populations and morphological plant types supports its use as a basis for the PAM.

The major effects of increased plant populations on individual plants within a crop were the suppression of branches and the decrease in PWT values. The decline in mean PWT values (Chapter 5) were interpreted in terms of the PAM, as indicating a negative shift of the mean coordinate of the ellipse down the principal axis towards the origin and SWT axis intercepts, as population was increased. The reduction in SD values for the SWT and PWT distributions were of a similar magnitude across plant populations and this was reflected in the stability of the gradients of the principal axes for each genotype. The dimensions of the ellipse decreased in proportion to the decreases in mean SWT and PWT values except at 225 and 400 plants m^{-2}. At these two highest populations the projected lengths on both axes were larger than anticipated from the changes in their mean values.

Over all treatments the PAM was a useful tool for describing the relationship between SWT and PWT values for field pea crops, even when significant changes in the distributions of these values occurred.

As plant populations increased, greater variability was found in the PHI values. This variability probably resulted from the change in the PWT range and consequently the increased influence of the MPW. For genotype CLU, the low MPW value may have contributed to the higher mean PHI values at 400 plants m^{-2}. In contrast, for genotype CVN the CV for PHI was approximately double those for other genotypes at 400 plants m^{-2}. The implications of these genotypic differences in the components of the PAM are examined in greater detail in Chapter 8.

The detection of the largest MPW at 9 plants m^{-2} was unexpected, but may have resulted from the higher degree of branching at this population. It follows, that the aim of producing a non-competitive environment at 9 plants m^{-2} may have been achieved at the plant level of classification but not at the branch level.

In Chapter 7, the biological characteristics of the genotypes in this 1989/90 population experiment are examined, and related to differences in their total seed yields. In addition, the biological factors which influence individual plants within a crop are investigated with emphasis on the small plants which tend to have lower PHI values. Thus, the objective is to relate the location of individual points in the PAM to biological factors, with particular emphasis on the plants located closest to the PWT axis intercept.

CHAPTER SEVEN

BIOLOGICAL CAUSES OF DIFFERENCES IN PLANT AND GENOTYPE YIELDS

7.1 INTRODUCTION

Significant differences in seed yield were found among the genotypes in the 1989/90 plant population experiment. Genotype CVN produced the lowest yield at 400 plants m^{-2} and SVU produced a lower seed yield than CLU and SLU at both 225 and 400 plants m^{-2}. These yield differences were associated with differences in CHI and mean PHI values (Chapter 5). Lower harvest indices may result from lower partitioning of assimilate into seed for all plants in the crop, or they may occur because interactions between plants have induced poor partitioning for some individuals within the crop (Hedley and Ambrose, 1984). To ascertain which mechanism was dominant, or whether other factors contributed to variability in harvest index and therefore seed yield, it was necessary to analyze the structure of the plant populations.

The results in Chapters 5 and 6 indicated that both the variation in, and location of, the PHI distributions contributed to the lower seed yields for genotypes CVN and SVU. The CV for PHI in genotype CVN at 400 plants m^{-2} was approximately double the corresponding values from the other genotypes (Table 6.5), which indicates that CVN had the greatest variability in PHI values among plants. In contrast, for SVU the CV for PHI was similar to the higher yielding genotypes but the mean PHI was lower.

In this chapter, the main aim is to identify biological contrasts among the genotypes that may have contributed to these seed yield differences. Specifically, the objective is to relate differences in the growth and development of genotypes (namely, the mean number of DAS to emergence, flowering and maturity, and measurements of seedling vigour) to the seed yield differences found among these crops at the two highest plant populations.

A second aim is to examine the factors that influenced individual plant performance within each crop. The emphasis is on the small plants that tended to have lower PHI values. In particular, the objective is to relate the location of individual points in the PAM to biological factors, with emphasis on the points located closest to the PWT axis intercept. The influence of pre-emergence sources of variation (Benjamin and Hardwick, 1986; Section 2.5.2) on PWT are interpreted from analyses of the date of emergence for individual plants. The effects of post-emergence sources of variation on PWT are interpreted from measurements of seedling vigour, competition from neighbours and viral infection.

In Section 7.2 the materials and methods are described. The methods were chosen to allow non-destructive measurements within each crop, and therefore to enable the same plant to be measured repeatedly. The results are summarized in Section 7.3 and discussed in Section 7.4.

7.2 MATERIALS AND METHODS

7.2.1 Experimental Details

The experimental details of design, genotype selection, site, soil preparation, plot sizes, plant numbers, crop husbandry and measurements made on individual plants (SWT, PWT and viral damage) were outlined in Section 5.2. In addition, the length of the main

stem was measured at harvest, and soil temperatures, at a 50 mm depth, were obtained daily from a weather station approximately 100 m from the experiment site.

7.2.2 Measurements

7.2.2.1 Crop development. The development of each crop was monitored throughout the season and described using growth stages defined by Knott (1987). Emergence was recorded when the first visible signs of the plumule were observed above the soil, or code 004 (Knott, 1987). Emergence was recorded daily for each plot to determine the number of DAS to emergence for each plant. Observations were made for 25 DAS after which video records were used to monitor any further emergence (Section 7.2.2.3)

The vegetative phase of growth was defined for each crop as the number of DAS to the first open flower (203; Knott, 1987). The reproductive phase was measured as the number of days from this first flower to harvest maturity, when all pods were dry and brown and seeds were dry (303; Knott 1987). The duration of growth was defined as the number of DAS to harvest maturity.

7.2.2.2 Seedling growth. Thirty-two days after sowing, a random selection of four plants was harvested from the boundary rows of each plot from replicates 1 and 3, to represent the two planting dates. Measurements of plant height, plant weight, leaf area and physiological development were made. From these measurements, and the video records of ground area cover (Section 7.2.2.3), ratios of height per unit dry weight, leaf area per unit dry weight and ground cover per unit dry weight were calculated for each genotype.

7.2.2.3 Ground area cover from individual plants. The vegetative growth of all labelled plants (Table 5.1) was recorded at 7-10 day intervals, on to 8 mm

video tape using a Sony Handicam video recorder. The video records commenced 30 DAS for replicates 1 and 2 and 20 DAS for replicates 3 and 4. The aim was to assess plants from each replicate at approximately the same stage of physiological development. This meant recordings were 7-10 days later for replicates 1 and 2 than in replicates 3 and 4. The mean number of DAS for each recording date was therefore calculated and used in the presentation of results for ground cover.

To record the video images, a moveable platform approximately 0.5 m high was positioned across each plot. Images were then recorded by a hand-held camera, positioned directly above each plant, from a height of approximately 1.8 m. This process was continued for all plants in each crop until the overlap of leaves prevented measurement of individual plants within the crop. Overlap did not occur in the 9 and 49 plants m^{-2} treatments, and recording was stopped when the height of plants prevented placement of the platform across the plots.

The video records were analyzed by selecting individual frames from the tape for conversion to computer images using an image analyzer (Magiscan, Joyce-Loebl Ltd, Tyne and Wear, England). A light pen was used to trace around the leaf edges of plants, and the enclosed area was measured, to obtain an estimate of the ground surface area covered by each plant. After comparing three analogue and two microprocessor based methods for estimating leaf area, Beerling and Fry (1990) concluded that image analysis and leaf area meters provided the best compromise between accuracy, variability and time taken to make measurements.

Data for ground cover in each plot, was collected from the video records for the five plants that had the lowest PWT at harvest. These plants were collectively defined as the 'small' plants. A further five plants were selected randomly to represent the remaining 'standard' plants in each plot. From these latter plants, 95 % confidence intervals were calculated for the mean PWT. The true population mean PWT, previously calculated for all plants in each plot, was found within 79 of the 80 intervals. The five sampled plants were therefore considered to be representative of their respective plots.

7.2.3 Statistical Analysis

7.2.3.1 Crop development. The emergence data from replicates 1 and 2 were analyzed separately from replicates 3 and 4 due to the 16 day difference in the planting dates. Analysis of variance for emergence was subsequently based on the split-plot design described in Section 5.3.2 (Table 5.9), but with two replicates per planting date.

Analysis of the total duration of crop growth, and the lengths of the vegetative and reproductive phases, were based on the analysis of variance for the split-plot design with four replicates, without the separation for individual plants. Mean separation for all variables was based on least significant difference tests.

7.2.3.2 Seedling growth. Results from the destructive harvests of seedlings (Section 7.2.2.2) were analyzed separately for each planting date using a one way analysis of variance (Minitab, 1989). Comparisons among genotypes were made from 95 % confidence intervals using pooled standard deviations.

7.2.3.3 PWT and date of emergence. Examination of the relationship between the PWT at harvest and date of emergence of individual plants involved expanding the split-plot model to include the date of emergence as a treatment. Date of emergence was therefore the fourth treatment in the model.

The analysis of variance for this relationship was run separately for each of the two planting dates. The effects of emergence date, and the interactions of genotype with emergence date, and population with emergence date were assessed using the Type III sum of squares rather than Type I. It was necessary to use Type III sums of squares because the data for each emergence date were unbalanced, with different numbers of observations for each date. The varying number of observations also affected SEM calculations for emergence date. In addition, the emergence date was not a fixed factor

in the design of the experiment and could only be included after emergence results were recorded. Thus, results from these analyses are presented as indicating trends among treatments without strong emphasis on the statistical differences.

7.2.3.4 Ground cover. Analysis of ground area cover from individual plants was based on the full split-plot design (Table 5.9), and was conducted separately for the 'standard' and 'small' plants. Small plants that had not emerged at the time of recording were considered as missing data to reduce their influence on the mean ground cover values from the plot.

The analysis was run on a VAX computer using the *'PROC GLM'* from the *'SAS'* statistical package (SAS Institute, 1990). The analysis was run separately for each planting date. The effects of emergence date, the interactions of genotype by emergence date, population by emergence date and genotype by population by emergence date were assessed using the Type III sum of squares.

7.2.3.5 Neighbourhood competition. The analysis of interplant competition within a crop was adapted from methods outlined by Besag and Kempton (1986) to analyze inter-plot competition. The PWT of each individual plant was related to the mean PWT of its four nearest neighbours. The 'on-the-square' planting arrangement meant that the linear distance between the central plant and its nearest neighbours to the north, south, east and west was equal.

The requirement to have four neighbours around each analyzed plant meant that the number of plants available for analyses varied among populations. This occurred both because the plants on the perimeter of the labelled control area in each plot could not be used (they had no neighbours) and because the arrangement of labelled plants differed among populations (Table 5.1). For example, at 9 plants m^{-2} the 60 tagged plants were arranged in 12 rows of 5 plants. This allowed 10 rows of 3 plants (30 plants) to be

included in the analysis. Thus, analyses included 30, 64, 66, 60 and 54 plants at 9, 49, 100, 225 and 400 plants m^{-2} respectively.

7.2.3.6 Viral infection. The impact of viral infection on individual plants was examined by comparing the PHI values and the relationship between SWT and PWT from analyses which both included and excluded the infected plants.

7.3 RESULTS

7.3.1 Crop Development

7.3.1.1 Emergence. Emergence was at least 94 % for all genotypes at both planting dates. The effects of replicate and genotype on the number of DAS to emergence differed between planting dates, but there were no significant interactions between either genotype, replicate or population for either planting date.

The mean emergence date was 8.7 DAS for the first planting date, with about 94 % of the plants that emerged present 11 DAS, and 96 % present 14 DAS (Table 7.1). On average, emergence was quickest for genotype SVU (8.4 DAS) and slowest for SLU (9.2 DAS). There were no significant replicate ($p=0.261$) or population ($p=0.373$) effects. In comparison, the mean emergence date was 10.3 DAS for the second planting date, with between 65 and 86 % of the plants present 11 DAS and 97 % after 14 days (Table 7.1). Genotype SVU again had the earliest mean emergence (9.6 DAS) and SLU was slowest, averaging 11.0 days to emergence (Table 7.1). Emergence was about half a day later ($p<0.05$) in replicate 3 than replicate 4.

Between 0 and 5 % of the plants in each of the plots emerged later than 14 DAS (Table 7.1), with some emergence as late as 34 DAS. The 259 plants that emerged at least 14 DAS were grouped together and defined as late emerging in the analysis of the relationship between PWT and emergence date (Section 7.2.3.2).

Table 7.1: Daily emergence (% of final) for field pea genotypes sown at two planting dates in the 1989/90 experiment. *Late plants were those emerging later than 14 days after sowing. †Mean number of days to emergence for each genotype. Values with a letter subscript in common are not significantly ($p<0.05$) different within each planting date. The standard errors of the mean emergence dates were 0.16 days for the first planting date and 0.08 days for the second.

	Number of days after sowing to emergence								
	8	9	10	11	12	13	14	*Late	†Mean
Genotype	First planting date								(days)
CVN	58.5	85.1	92.7	93.3	94.5	95.1	95.1	100	8.5_b
CLU	47.6	82.2	92.9	94.7	95.5	96.3	96.7	100	8.7_{ab}
SVU	68.8	89.7	93.7	94.5	95.3	95.9	96.5	100.1	8.4_b
SLU	22.8	63.6	87.4	92.7	94.1	94.7	95.3	100	9.2_a
	Second planting date								
CVN	16.9	34.6	59.7	81.1	91.8	94.5	96.3	100.1	10.2_b
CLU	15.2	32.7	55.2	76.0	89.6	93.5	97.4	100.2	10.4_b
SVU	29.3	53.4	73.6	86.2	94.5	96.4	97.9	99.8	9.6_c
SLU	4.5	16.8	28.4	65.0	89.6	95.3	97.6	99.9	11.0_a

7.3.1.2 Seedling growth. The analyses of seedling growth for both planting dates showed that, on average, vigorous genotypes were significantly taller, heavier and had greater leaf areas than the low vigour genotypes. For example, for replicate 1 the mean plant height for CVN was 107 mm, and the mean weight was 0.26 g, with a leaf area of 3960 mm^2. In comparison, the mean height, weight and leaf area for CLU were 61 mm, 0.17 g, and 2540 mm^2, respectively.

However, when these results were converted to plant height and leaf area per unit dry weight, no significant differences were found between the vigorous and low vigour genotypes of each plant type. For example, the ratio of plant height to weight for CVN was 0.41 mm mg^{-1} compared to 0.38 mm mg^{-1} for CLU ($p=0.15$), and for leaf area, the ratio was 15.2 mm^2 mg^{-1} for CVN and 15.4 mm^2 mg^{-1} for CLU ($p=0.61$). A similar result was observed from the ground cover results with no significant differences ($p=0.12$) in the ratio of ground cover per unit dry weight, which ranged from 6.2 (SVU) to 7.4 mm^2 mg for CVN.

Although plants were harvested at 32 DAS for both replicates, those from replicate 3 had approximately double the height, weight and leaf area of plants from replicate 1. In addition, classification of the physiological development (Knott, 1987) showed that plants from replicate 3 had developed to stage 106.5 compared to 103.6 for replicate 1.

7.3.1.3 Growth duration. The analyses of phenological development showed significant ($p<0.01$) replicate, genotype and population effects, but no significant interactions. The duration of the vegetative phase ranged from 54.5 days for replicate 3 to 56.4 days for replicate 1 (Table 7.2). Harvest maturity was reached about 114 DAS for replicates 1 and 2, but 106 DAS for replicates 3 and 4 (Table 7.2).

Table 7.2: Mean duration of vegetative and total crop growth for crops grown in the 1989/90 plant population experiment. Values within a section of the table with a letter subscript in common are not significantly ($p<0.05$) different.

	Vegetative growth (days)	Total crop growth (days)
Replicate		
1	56.4_a	113.4_a
2	55.6_b	114.6_a
3	54.5_d	106.0_b
4	55.0_c	105.3_b
(SEM)	0.16	0.53
Genotype		
CVN	59.0_a	108.9_b
CLU	58.5_a	110.2_b
SVU	48.9_c	106.9_c
SLU	55.2_b	113.2_a
(SEM)	0.16	0.53
Population (plants m^{-2})		
9	57.9_a	119.3_a
49	56.1_b	111.6_b
100	55.3_c	107.6_c
225	54.0_d	105.6_d
400	53.6_d	104.9_d
(SEM)	0.18	0.60

Flowering occurred about 59 DAS for the two conventionally leafed genotypes (Table 7.2) but was significantly earlier for SLU (55.2 DAS) and SVU (48.9 DAS). Genotype SLU took approximately 6 days longer to reach harvest maturity than SVU (Table 7.2), which meant a similar duration (58 days) for their reproductive phases.

Increased plant population resulted in shorter vegetative and reproductive phases. On average, harvest maturity was reached 119.3 DAS at 9 plants m^{-2} compared to 104.9 DAS at 400 plants m^{-2}.

7.3.2 Effect of Population and Emergence Date on PWT

Responses for PWT were similar for both planting dates, so only the results for the first date are presented in Table 7.3. Plant population was the most influential determinant of PWT (discussed in Chapter 5). The plant population also affected the relationship between the mean PWT of small plants and the mean PWT for each population. At 9, 49 and 100 plants m^{-2} the mean PWT of the small plants was about 33 $\pm$ 1.6 % of the mean PWT for each population. This dropped ($p<0.01$) to 21 $\pm$ 1.3 % at the two highest populations.

The results for PWT also showed there was a significant interaction ($p<0.01$) between the effects of emergence date and plant population. In general, the mean PWT at harvest declined as the number of DAS to emergence increased. However, the magnitude of the decline was higher at the higher plant populations (Table 7.3). For example, the late emerging plants at 9 plants m^{-2} had mean PWTs that were about 50 % of the PWT for plants emerging in less than 12 DAS. In comparison, the PWTs achieved by the late emerging plants at 225 and 400 plants m^{-2} were only about 20 % of those for plants emerging up to 12 DAS (Table 7.3).

The validity of the association between date of emergence and PWT was, however, limited by the unequal numbers of plants at each emergence date and, in particular, by the low number of observations for late emerging plants (Table 7.3).

Analyses of the PWT data for late emerging plants showed 48 % of them were also classified as 'small' plants and a further 18 % died after emergence. Of the 46 plants that died after emergence, 39 were late emerging with 29 of these emerging at least 25 DAS.

7.3.3 Ground Cover from Individual Plants

No significant interaction effects were found for the ground cover results at any of the four recording dates. Results are therefore presented for the main effects of replicate, genotype and plant population. A confounding factor for these results was that the overlapping of leaves among plants which occurred at different times for each genotype. In particular, measurements were not taken at 39 DAS for genotype CVN at 225 plants m^{-2} or CVN, CLU or SVU at 400 plants m^{-2}. At 44 DAS CVN was not measured at 100 plants m^{-2} and only CLU was measured at 225 plants m^{-2}. No measurements were possible at 400 plants m^{-2}. A breakdown of the data into genotype by population interaction tables showed that the general trends observed from the main effects were consistent for each genotype at each population. Results are therefore only presented for main effects with a caution that the apparently larger values for genotype CVN at 45 DAS were accentuated by the lack of data from the higher populations of this genotype.

7.3.3.1 Replicate effect. A significant replicate effect was observed for ground cover at the first recording date. Standard plants from replicates 1 and 2 covered about 20 % more ground area than from replicates 3 and 4 (Table 7.4). This effect was consistent with the difference in the dates of recording, which were 30 DAS for the first two replicates (103-105; Knott, 1987) and 20 DAS (102-104; Knott, 1987) for replicates 3 and 4. For subsequent recordings there was no significant difference among replicates for ground cover of the standard or small plants, even though plants from replicates 1 and 2 were 7-8 days older than those from replicates 3 and 4.

Table 7.3: Effect on mean PWT (g) of field pea plants from different plant populations and emergence dates. Data are for plants from replicates 1 and 2 of the 1989/90 plant population experiment. *Late plants emerged later than 14 days after sowing. The standard error of the mean (SEM) was 8.84 g at 9 plants m^{-2} and 6.85 g from 49 to 400 plants m^{-2}. SEM values were not calculated for emergence data because of the large variations in the number of observations (n) at each date.

Population	Number of days after sowing to emergence							
(plants m^{-2})	8	9	10	11	12	13	14	*Late
9	76.3	76.2	73.4	69.4	61.1	35.7	69.0	36.2
49	22.2	21.9	23.1	23.4	17.6	18.4	20.6	8.1
100	13.0	12.9	13.3	10.7	12.2	11.8	7.4	4.8
225	5.60	5.75	5.33	6.64	4.12	7.00	0.85	1.03
400	3.61	3.52	3.56	3.95	3.35	1.75	0.65	0.92
(n)	1653	1027	388	70	31	24	14	259

Table 7.4: Mean ground area covered (mm^2) by individual 'standard' plants from each replicate in the 1989/90 plant population experiment. Values within acolumn with a letter subscript in common are not significantly ($p<0.05$) different.

	Recording date (days after sowing)			
Replicate	25	32	39	44
1	1350_{ab}	1648_{a}	3634_{a}	5146_{a}
2	1431_{a}	1881_{a}	3401_{a}	5242_{a}
3	1069_{c}	1817_{a}	3240_{a}	6520_{a}
4	1110_{bc}	2227_{a}	3956_{a}	-
(SEM)	171.3	140.7	361.8	408.4
(p value)	0.02	0.11	0.55	0.16

7.3.3.2 Genotype effect. There was a significant genotype effect found for the ground cover from standard plants at each recording date. On average, the area covered by individual plants of genotype CVN was about 30 % larger ($p<0.05$) than the other genotypes at each recording date (Table 7.5). In addition, the area covered by the semi-leafless vigorous genotype (SVU) was always higher than that covered by the semi-leafless low vigour genotype (SLU), although not significantly.

Similar ground cover results were observed for the small plants. Values were 40-50 % higher for CVN than the other genotypes, and the ground area covered by genotype SVU was generally greater than by SLU (Table 7.5). A comparison of ground cover between the standard and small plants shows that the standard plants consistently covered about 30 % more area than the small plants.

Table 7.5: Mean ground area covered (mm^2) by individual 'standard' and 'small' plants of each genotype in the 1989/90 experiment. Values within a column with a letter subscript in common are not significantly different ($p<0.05$) within each section of the table.

Genotype	Recording date (days after sowing) 25	32	39	45
	Standard plants			
CVN	1632_a	2541_a	5242_a	9045_a
CLU	1182_b	1616_b	3321_b	5419_b
SVU	1077_b	1881_b	3513_b	4840_b
SLU	1061_b	1640_b	2766_b	3988_b
(SEM)	77.2	140.7	361.0	408.4
	Small plants			
CVN	1126_a	1704_a	3248_a	5925_a
CLU	868_{ab}	1101_b	1865_b	2983_b
SVU	740_b	1262_b	2203_b	2525_b
SLU	796_b	1077_b	1640_b	1809_b
(SEM)	82.0	89.2	233.2	513.0

7.3.3.3 Population effect. At the first recording date there was no apparent trend in ground cover across populations. Ground cover by the standard plants at 225 plants m^{-2} was higher than at 9, 49 and 400 plants m^{-2} (Table 7.6). In contrast, the ground area covered by small plants at 9 and 225 plants m^{-2} was higher than that at 100 plants m^{-2}.

At the remaining three recording dates the population effect was significant for the standard plants (Table 7.6). Ground cover was greatest by individual plants at 9 plants m^{-2}, although this cover from individual plants only amounted to a total crop cover of

6 %, 44 DAS (Table 7.6). Ground cover per plant declined as population increased with the lowest cover found at 400 plants m^{-2}, and this represented a total crop cover of about 59 %, 44 DAS (Table 7.6). The results for small plants followed similar trends to the standard plants, with ground cover per plant decreasing as plant population increased (Table 7.6).

Table 7.6: Mean ground area covered (mm^2) by individual 'standard' and 'small' plants at each plant population in the 1989/90 experiment. †Numbers represent approximate percentage crop ground cover 45 days after sowing. Values within a column with a letter subscript in common are not significantly ($p<0.05$) different within each section of the table.

Population (plants m^{-2})	Recording date (days after sowing) 25	32	39	45	†Crop cover (%)
	Standard plants				
9	1190_b	2155_a	4399_a	6520_a	5.9
49	1222_b	2082_b	4012_a	5540_b	27.1
100	1238_{ab}	2018_b	3505_b	3272_c	32.7
225	1351_a	1696_b	2227_c	2621_d	59.0
400	1206_b	1463_b	1664_c	-	-
(SEM)	57.1	84.4	145.5	257	
	Small plants				
9	965_a	1568_a	2983_a	4125_a	3.7
49	884_{ab}	1375_{ab}	2179_b	2508_b	12.2
100	732_b	1182_b	1833_{bc}	2010_b	20.1
225	925_a	1142_b	1391_c	1761_b	39.6
400	836_{ab}	989_b	1447_{bc}	-	-
(SEM)	57.9	87.6	211.5	288.9	

7.3.4 Nearest Neighbour Analysis

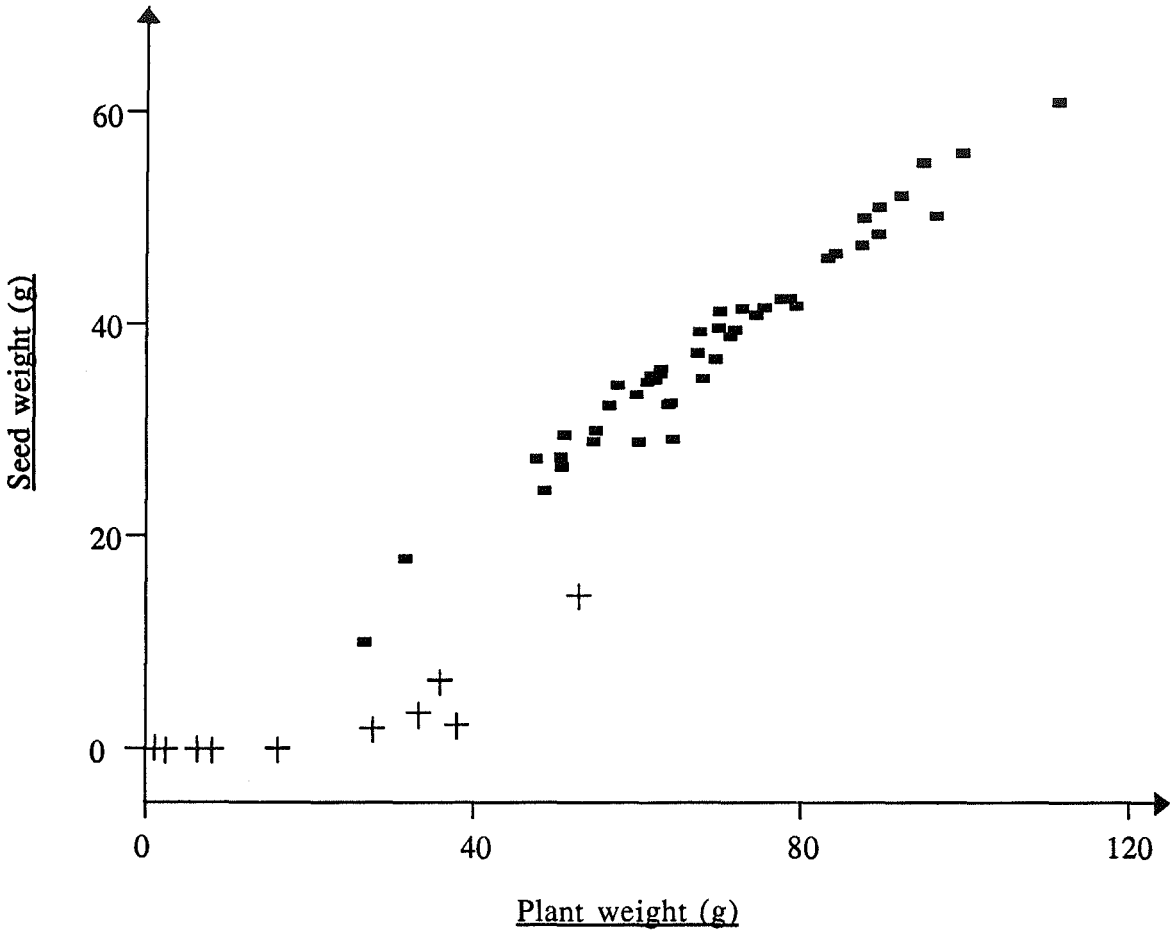
The influence of neighbours on PWT varied among plots. There was no significant relationship in 61 of the 80 plots; their R^2 values were between 0 and 6 %. The R^2 values were between 10 and 20 % for 16 of the remaining 19 plots, and the highest R^2 of 25.3 % was found for replicate 3 of genotype CLU at 9 plants m^{-2}.

7.3.5 Virus Infection and Individual Plant Performance

Infection by cucumber mosaic virus affected the vegetative and reproductive performance of some plants, and influenced the relationship between their SWT and PWT. Of the 216 infected plants, 94 were barren and a further 97 had a PHI $\leq$ 33 %. The maximum PHI was 57.7 % from a single infected plant. Generally, infected plants also had low PWT values and were therefore located near the PWT axis intercept of the principal axis.

The results for replicate 1 of genotype SVU at 9 plants m^{-2} are presented to illustrate the effects of the infected plants on the relationship between SWT and PWT. The 10 infected plants in this crop were either barren (5 plants) or poor performing, and all had low PWT values (Figure 7.1). A comparison of the regression equations showed that when the infected plants were included, the SWT axis intercept decreased from -2.31 to -7.36, the gradient increased from 0.58 to 0.64 and the residuals approximately doubled, with R^2 values dropping from 96.5 % to 92.4 %.

Figure 7.1: Relationship between seed weight and plant weight of virus infected plants (+) and non-infected plants (■). Data is from replicate 1 of genotype SVU sown at 9 plants m^{-2} in the 1989/90 plant population experiment.



7.4 DISCUSSION

The discussion is separated into two sections. In the first, the biological causes of the seed yield differences among genotypes at 225 and 400 plants m^{-2} are investigated (Section 7.4.1). In the second part, the within crop causes of variability in individual PWT and PHI values are examined (Section 7.4.2).

7.4.1 Genotypic Differences in Crop Growth

7.4.1.1 Emergence and plant growth. The initial selection of genotypes for this study was based on qualitative assessments of their seedling growth (Table 3.1). Following this selection it was found that at high plant populations, both genotypes that showed vigorous seedlings growth (CVN and SVU) had lower seed yields than the genotypes with seedlings of low vigour (CLU and SLU). It is therefore important to quantify 'vigour' for possible use as a selection criterion.

Both the emergence data and ground cover results highlight differences among the genotypes that were consistent with these original classifications of vigour. The mean emergence dates for the vigorous genotypes were earlier than for the low vigour genotypes, particularly for SVU (Table 7.1).

The consistency of these results for all plant populations at both planting dates, indicates that an intrinsic source of variation exists among the genotypes. Other authors have suggested that differences in the embryonic axes (Pyke and Hedley, 1983; Hedley and Ambrose, 1985) or pre-emergence growth rates (Benjamin and Hardwick, 1986) are responsible for differences in emergence. In addition, the later emergence of plants from SLU, with the highest 1000 sw (Chapter 6), suggests that large seed size and the associated advantage in seed reserves does not necessarily lead to faster emergence of plants.

The 1-2 day later emergence for the second planting date was attributable to differences in soil temperatures. Using a base temperature of 1.4 °C for peas (Angus *et al.*, 1980), 76.6 heat units were accumulated, at a soil depth of 50 mm, in the 8 DAS for the first planting date. However, it took 9-10 DAS to accumulate the same number of heat units from the second planting date (Table 7.7). This suggests that pea seedling emergence takes a constant amount of thermal time and that its value is genotype specific as found for other crops (Emerson and Minor, 1979).

Table 7.7: Daily soil temperatures (°C) following the sowing of the 1989/90 experiment. Measurements are 9.00 am readings at a soil depth of 50 mm from a weather station located about 100 m from the experiment site.

Days after sowing	Planting date	
	23/24 Sept	9/10 Oct
	Soil temperature (°C)	
1	8.6	11.5
2	11.0	8.5
3	11.6	11.4
4	11.7	9.6
5	11.5	10.8
6	12.1	10.5
7	14.5	9.1
8	12.6	8.6
9	12.0	8.6
10	11.2	10.5
11	6.6	12.4
12	7.5	12.0

There were also replicate differences for the stage of development 32 DAS, and the total duration of crop growth. The destructive harvest showed that plants from the second planting date had three more vegetative nodes than plants of the same age from the first planting date (Section 7.3.1.2). In addition, the total duration of growth was about 7 days shorter for the second planting date (Table 7.2). The implication is that the phenological development, which depends on temperature and photoperiod (Wilson, 1987), was faster for the later sown crops.

The variation in emergence dates between vigorous and low vigour genotypes was maintained into seedling growth as indicated by differences in plant height, weight and ground cover. Plants of genotype CVN were approximately double the height and weight of plants from CLU at both harvest dates. In addition, the ground cover from CVN was about 40 % more ground area than plants of CLU at each recording date. Similar results for height, weight and ground cover were found for comparisons of the vigorous genotype SVU with SLU.

It follows that the classification of vigour, used to screen these genotypes in 1988/89 (Chapter 3), was related to a visual assessment of the seedling size, as measured by the height, weight and ground cover, within each plot. Future screening for vigour of genotypes could be quantified by comparisons of these measurements for individual plants.

Data from recording 39 DAS indicated earlier canopy closure for the vigorous genotypes. That is, at about 39 DAS measurements were taken for crops of CLU at 225 plants m^{-2}. However, identifying individual plants within crops of genotype CVN was impossible at this population (Section 7.3.3), due to the overlapping of leaves from neighbouring plants. Similarly, plants from SLU were able to be measured at 400 plants m^{-2} but measurement was impossible for SVU.

There were differences in all three methods of measuring seedling size among genotypes. This implies that the vigorous ones either had an advantage in the spatial distribution of their leaves, or had higher relative growth rates than the low vigour genotypes. The results from the two destructive harvests of seedlings at vegetative stages 103.6 (replicate 1) and 106.5 (replicate 3) showed that the vigorous genotypes were taller, heavier and had greater leaf areas (Section 7.3.1.2) and ground area cover (Table 7.5) than the low vigour genotypes. However, the ratio of height per unit dry weight, leaf area per unit dry weight and ground cover per unit dry weight were similar for each plant type.

Thus, these results indicate there was no advantage in the spatial arrangement of leaves, with respect to total above ground dry biomass, for the vigorous genotypes over the low vigour genotypes. It follows, that at some stage prior to these measurements, the vigorous genotypes had a greater above ground relative growth rate than the low vigour genotypes.

7.4.1.2 Comparisons of growth among genotypes. A consequence of their higher growth rate is that canopy closure would occur earlier for the vigorous genotypes. Given the similarity in the total duration of growth for CVN and CLU, this earlier canopy closure results in greater PAR interception during the season by CVN. It follows from Equation 7.1 (Charles-Edwards, 1982):

$$TBY = E \times Q \qquad \text{Equation 7.1,}$$

where TBY is the biological yield, E is the conversion efficiency of PAR to dry matter and Q is the amount of PAR intercepted, that if values of 'E' were the same, then the greater PAR interception should result in a greater biological yield.

Increased TBY with greater PAR was evident for all genotypes at populations from 9 to 100 plants m^{-2}, where the amount of PAR intercepted was the dominant component in determining the biological yield of crops. However, results from this study indicate that

there were differences in the conversion efficiency (E) between the conventional genotypes. Given the similarity in the total duration of growth for CVN and CLU (Table 7.2), the earlier canopy closure for CVN results in greater PAR interception and therefore a higher value of Q for CVN. In order for CVN to produce significantly less biological yield (17 %) than CLU (Figure 5.2), with an equal or larger value of Q, the conversion efficiency (E) of CVN must have been less than that for CLU.

A similar result occurs when the energy values of the biological yield is considered. Following methods outlined by McDermitt and Loomis (1981) the energy content of dry matter from CVN was calculated to be about 15 % lower than CLU. A comparison of values of E for pea crops indicates differences of 10-20 % both within and between experiments. Heath and Hebblethwaite (1987) report E as 1.90 g of DM per MJ PAR for Øyjord drilled plots, compared to 1.65 g of DM per MJ PAR for precision drilled crops, while Wilson *et al.* (1985) estimated E at 2.36 g of DM per MJ PAR, although both reports indicate genotypic differences in E were low.

A higher respiration rate could explain both the increased ground cover during seedling growth and the lower biological yield at 400 plants m^{-2} for genotype CVN. Other explanations, such as more efficient photosynthesis rates, have difficulty fulfilling both of these results at the same time. If genotype CVN had a higher respiration rate than CLU, with a similar or lower gross efficiency, then the higher relative growth rate achieved by its seedlings would be due to a faster utilization of resources by individual plants. However, if the respiration rate remained high at full light interception, then a wastage of resources would result. Identifying the exact causes of these yield differences in the conventional genotypes requires detailed physiological studies, including measurement of PAR interception.

Interpreting the results for the semi-leafless genotypes, in terms of Equation 7.1, is complicated by several factors. Although these genotypes attained the same biological yield at 400 plants m^{-2}, the seed yield and energy content of the dry matter produced by

SLU were higher than for SVU. In addition, any advantage in PAR interception, due to earlier canopy closure by SVU, would have been offset to some extent by its shorter duration of growth (Table 7.2). Thus, quantifying any differences in PAR interception between these semi-leafless genotypes is not possible from the data obtained for this study. Therefore no inferences can be made about any possible differences in PAR interception or conversion efficiency.

In summary, the data from this study indicates that at 400 plants m^{-2} genotype CVN intercepted a greater amount of PAR than CLU but produced 17 % less dry matter. This implies there were differences in the conversion efficiency of these two genotypes. In contrast, a combination of several factors influenced the differences in seed yield of the semi-leafless genotypes, including differences in their seedling vigour and the duration of crop growth.

7.4.2 Factors Affecting Individual Plant Performance

The second part of this discussion examines the individual performance of plants within a crop. The emphasis is on identifying the impact of delayed emergence, seedling vigour, interplant competition and virus infection on PWT and SWT values.

7.4.2.1 Emergence date. About 94 % of the plants that emerged from all crops were present within four days of initial emergence. The PWT values attained by these plants were consistent at each population regardless of the day of emergence (Table 7.3). However, for plants that emerged after this initial four day period, there was a decrease in PWT. This reduction was most apparent for the late emerging plants and was also influenced by plant population. This result is consistent with the proposal of partial asymmetric competition of Benjamin (1990) and indicates that the late emerging plants tend to become the smaller plants in the population. Soetono and Donald (1980) reported a similar result for barley plants, with a 3 day delay in emergence resulting in a 43 % reduction in the number of grains formed.

Interplant competition appeared to accentuate the differences in emergence dates. The late emerging plants from high populations achieved PWTs which were only about 20 % of those from earlier emerging plants. Thus, the earlier emerging plants probably acquired a disproportionate share of resources and were heavier and more competitive at the onset of interplant competition (Benjamin and Hardwick, 1986).

An indication of the impact of interplant competition can be gained by comparing the PWT reduction for late emerging plants at high and low populations. At 9 plants m^{-2}, where interplant competition was negligible, the PWTs of late emerging plants were about 50 % of those from early emerging plants. The implication from this result is that intrinsic factors, such as lower relative growth rates, were responsible for about 50 % of the reduction in PWT associated with late emergence. The contribution of interplant competition at the two highest populations was therefore estimated to reduce PWTs by an additional 30 % (Table 7.3).

A breakdown of the PWT data for late emerging plants also highlighted the influence of delayed emergence. Although these late emerging plants only represented about 5 % of the population they represented 48 % of the 'small' plants and 39 of the 46 plants which died after emergence. However, the results also show that delayed emergence did not automatically result in low PWT and 'small' plants were not always late emerging.

7.4.2.2 Ground area cover. The ground area covered by individual 'small' plants was consistently about 30 % lower than standard plants at all four recording dates, for each genotype (Table 7.5) and population (Table 7.6). The lower ground cover by 'small' plants is consistent with their generally later emergence. Several factors may contribute to the differences in seedling growth. If these small plants were planted deeper than average, more of the reserves from their cotyledons would be used in pre-emergence growth. For similar sized seeds, the resources available for vegetative growth would then be lower for the deeper sown seeds (Shanmuganathan and Benjamin, 1992).

Alternatively, the lower ground cover by the 'small' plants may reflect a lower relative pre-emergence growth rate, that continued into seedling growth.

A comparison of the ground cover results from spaced plants and those at higher populations gives an indication of when interplant competition began within each population. The results (Table 7.6) indicate that interplant competition was present at about 32 DAS for the two highest populations, and 39 and 45 DAS for 100 and 49 plants m^{-2} respectively. Assuming the same factors were responsible for producing small plants at each population, then a similar trend in the ground cover results is expected for the small plants.

However, significant differences in ground cover were detected for small plants about 10-14 days earlier than for the standard plants at each population. These differences in ground area cover between standard and small plants may reflect differences in the factors responsible for the retrospective classification of small plants at each population. Support for this hypothesis was inferred from the mean PWT results at each population. Small plants from the 225 and 400 plants m^{-2} populations only achieved mean PWTs that were about 21 % of the population mean, compared to 33 % for the three lower populations. This indicates that either different factors were responsible for the classification of 'small' plants or that the impact of the same factors varied across populations.

For example, delayed emergence may have been a primary cause of small plants at all populations. However, at high populations, where interplant competition occurred earlier in the season, the impact of delayed emergence on the PWT would be greater than at low populations.

7.4.2.3 <u>Neighbourhood competition.</u> Generally, models of neighbourhood competition are concerned with the space available to an individual plant and the activity of its neighbours (Benjamin and Hardwick, 1986). However, in this study, the 'on-the-

square' planting pattern meant the space available to each plant was equal within each population. The analysis therefore concentrated on the influence of neighbouring plants, rather than the influence of the available space.

The analyses of neighbourhood competition were inconclusive. For most plots there was no significant relationship between the PWT of an individual and that of its neighbours. Thus, although substantial competition was evident, from the changes in mean PWT and competition indices across populations (Chapter 5), any additional variation in the PWT for an individual within the crop could not be attributed to the PWT of its neighbours.

This result appears at odds with the data for emergence and ground cover, which indicated that the PWT of small and late emerging plants in a crop was reduced at high populations. The implication was that the neighbours of these small late emerging plants acquired a disproportionate share of resources and this was expected to manifest in the nearest neighbour analyses. However, the analyses of nearest neighbours indicated that the overall competition from neighbouring plants did not affect the PWT of an individual. The small and late emerging plants in this analysis only represented a maximum of about 10 % of the data for any crop. Thus, any influence of neighbours on these plants was probably diluted by the abundance of data related to the remaining plants, where the individual PWTs could not be related to the PWTs of neighbours. To determine more precisely the influence of neighbours on an individual, an experiment with a less uniform planting pattern and differences in planting dates among seeds may be necessary.

7.4.2.4 Virus. Variation in PWT and SWT within a crop can also be caused by external factors such as crop management, moisture availability and plant diseases. The results from the infection of cucumber mosaic virus are presented as an example of these external influences. The PWT and SWT of virus infected plants were substantially lower than those of non-infected plants (Figure 7.1).

The PWT of infected plants was included in the nearest neighbour analyses. However, there was no indication that the neighbouring plants capitalized on the extra resources available from the reduced plant growth. If field peas are unable to readily adapt to the reduced competition of weak neighbouring plants, then yield potential is lost from the crop. Furthermore, some infected plants did produce seeds but many of these were shrivelled and of no economic value. Thus, the magnitude of yield reduction for virus infected plants and crops may be greater than was reported in this study. The conclusion is therefore that breeding for virus resistance should be a high priority.

7.5 SUMMARY

In this chapter the emphasis has been on biological sources of variation in seed yield between genotypes and between individual plants within each crop.

The comparison of genotypes indicated that the qualitative classification of vigour used as one criterion to select them, was probably based on seedling growth. In general, the vigorous genotypes emerged earlier and, 32 DAS, their seedlings were taller, heavier, and had greater ground cover than the low vigour genotypes. Furthermore, ground cover by the vigorous genotypes was consistently higher than by the low vigour ones, and probably reflects differences in their relative growth rates.

For the two conventional genotypes, the length of their reproductive phases and total duration of growth were similar, although at 400 plants m^{-2} significant differences in seed and biological yields were found. An explanation for these yield differences was that CVN had a lower conversion efficiency than CLU possible due to a higher respiration rate. The 15 % lower energy value for the dry matter from CVN was consistent with the explanation of a lower conversion efficiency. For semi-leafless genotypes, the differences in emergence dates, seedling growth, and the total duration of crop growth, confounded explanations of the yield differences.

Investigations of individual plant performance highlighted differences in the date of emergence as contributing to lower PWTs. Plants emerging within the initial four days had similar PWTs but later emergence was associated with lower PWTs at all populations. This reduction in PWT was accentuated by population, with 'small' plants at the two highest populations having proportionally lower PWTs than those at lower populations. Late emergence was also reflected in the ground cover results which were reduced for the 'small' plants within each crop. The implication was that larger plants in the population acquired a disproportionate share of the available resources or that partial asymmetric competition was present. Despite this hypothesis, the nearest neighbour analyses failed to find any relationship between the PWT of an individual and the PWT of its neighbours, even if the plant had been infected by virus.

CHAPTER EIGHT

GENERAL DISCUSSION

8.1 INTRODUCTION

A major aim of the breeding, selection and screening of field pea genotypes is yield improvement, with the goal of producing high yielding, stable cultivars with disease resistance and adaptability to many environments (Jermyn, 1987). However, yield instability within and between sites and seasons has been identified as a persistent problem in field pea crops (Hedley and Ambrose, 1981; White, 1987) even when agronomic variation is minimized (Ambrose and Hedley, 1984).

After measuring the performance of individual plants within crops, Ambrose and Hedley (1984) concluded that differences in seed yield could be associated with variability in PWT and PHI distributions. In particular, they hypothesized that to improve the seed yield of field peas, breeding programmes should aim to produce cultivars with stable high PHI values for all plants in a crop. Stable high PHI values may be attained when the individual plants within a crop are weak competitors. Ambrose and Hedley (1984) specified several phenotypic characteristics that should be incorporated into a plant ideotype to achieve PHI stability of field peas.

These ideas provided the basis for this study, which focused on the relationships between frequency distributions of PWT and PHI values, seed yields and phenotypic characteristics.

The study is based at the individual plant level (Whistler *et al.*, 1986), but aimed at explaining population yield effects. The central problem for the study is to convert the

description of all of the individuals to a simplified mean function and dispersion descriptors which can be utilized to examine genotype, environment and GXE effects and consequently optimize yields. This is different from much plant breeding which has concentrated on yield components, whole crop and individual gene effects with relatively little concern for frequency distributions.

The main objective of this study was to test the hypothesis that variability in seed yields of crops could be associated with specific plant types that result in variable distributions of PWT and PHI values. This hypothesis led to three areas of research that will be discussed in this chapter. Firstly, it was necessary to examine the extent of variability in PWT and PHI within crops, and to establish whether this variability was related to differences in seed yield (Section 8.2). Secondly, there was a need to formalise the relationships between SWT, PWT and PHI from this and previous studies, (e.g. Ambrose and Hedley, 1984). The objective was to produce a quantifiable and testable system that could be used to relate differences in crop yields to differences in SWT and PWT distributions based on individual plants (Section 8.3). Finally, possible selection criteria required assessment, to determine whether specific plant types or attributes could be identified from this approach to assist yield improvement in breeding programmes (Section 8.4).

8.2 VARIABILITY BETWEEN AND WITHIN FIELD PEA CROPS

The first main assumption of this project was that differences in seed and biological yields between crops could be related to variability in PWT and PHI distributions.

This assumption was investigated for crops grown at 100 plants m^{-2} by a comparison of results from the 1988/89 cultivar evaluation trial (Chapter 3) and the 1989/90 plant population experiment (Chapters 5-7). Further comparisons were made across a wide range of plant populations using the data obtained from the 1989/90 experiment.

8.2.1 Variability in Seed and Biological Yields Between Crops

The first step in relating differences in seed and biological yields to PWT and PHI distributions is to examine the yield variability between crops.

8.2.1.1 Yield comparisons at 100 plants m^{-2}. The problem of yield variability in field pea crops is highlighted by a comparison of the seed and biological yields between the 1988/89 and 1989/90 seasons. The four genotypes common to both trials, and sown at a target population of 100 plants m^{-2}, had a maximum seed yield of 413 g m^{-2} in 1988/89 (Table 3.2). In contrast, the seed yield ranged from 643 to 697 g m^{-2}, or was about 50 % higher, in the 1989/90 season.

The biological yields and, therefore, yield potential of the crops grown in the 1989/90 experiment were also 25 to 55 % higher than in 1988/89. For example, genotype CVN produced 765 g DM m^{-2} in 1988/89 (Table 3.2) compared to 1200 g DM m^{-2} in 1989/90 (Figure 5.2). One aim of this study was to identify possible mechanisms at the individual plant level which were associated with the variability in crop yields, and subsequently to offer methods to reduce this variability.

A primary factor was the differing crop management between these trials. In particular, the volume and timing of irrigation applications was a limiting factor for some plots in the 1988/89 cultivar evaluation trial because of poor uniformity of water application by the sprinkler irrigation system. The consequent water stress experienced by these plots probably had a large influence on their seed and biological yields. The difference between yields in 1988/89 and 1989/90 implies that inadequate management of the cultivar evaluation trial meant that the four genotypes did not express their full yield potential.

It follows that the validity of differentiating among the 60 genotypes in the trial, on the basis of seed yield must be questionable. The range of seed yields from the 60 genotypes was from 180 to 500 g m^{-2}. However, cultivar rankings were probably confounded by variable water availability and may not accurately reflect the true relative yield potentials of these genotypes. This is particularly relevant given that the four genotypes in the 1989/90 experiment yielded 20 % more than any genotypes in the cultivar evaluation trial in the previous season. Furthermore, Prihar and Stewart (1991) suggested that genotypes may respond differently to water stress. This implies that the level of reduced yield potential exhibited by different genotypes may not have been uniform for all genotypes in the cultivar evaluation trial.

Differences in the planting method and arrangement between the two trials could also have contributed to the yield differences. That is, the uniformity of sowing depth and planting arrangement from the 'on-the-square' hand planting in the 1989/90 experiment probably contributed to higher yields. Clearly hand sowing is not feasible on a commercial scale, but plant to plant variation in yield may be reduced by more uniform planting patterns (Rogers, 1977; Davies *et al.*, 1985), although Heath and Hebblethwaite (1987) report no yield improvement from precision drilling when compared with Øyjord drilled crops.

The results of the cultivar evaluation trial highlight the importance of adhering to crop management advice for field peas (Jermyn, 1984), to ensure that agronomic variability is minimized. Despite the limitations of the management of the 1988/89 trial, seed yields were similar to previous studies for field peas. For example, Falloon and White (1978) reported a seed yield range of 300 to 400 g m^{-2} at about 100 plants m^{-2} and Cousin *et al.* (1985) reported 500 g m^{-2} for conventionally leafed field peas. Hedley and Ambrose (1981) reported seed yields of 260 and 310 g m^{-2} for conventional and leafless field peas respectively, and between 240 and 430 g m^{-2} for three leafless genotypes (Ambrose and Hedley, 1984). For their three leafless genotypes, biological yield was about 800 g m^{-2}. However, biological yields are seldom measured in agronomic or cultivar evaluation studies on field peas, which implies that they are not considered important.

The seed and biological yields from the plant population experiment in 1989/90 were similar for all genotypes and were all about 50 % higher than in the previous seasons trial. This result demonstrates that all four genotypes have high yield potential when grown at 100 plants m^{-2}, provided they are managed well. The high yields also demonstrate that the aim of minimizing the effects of agronomic factors on yield variability was achieved successfully in the 1989/90 trial. This was necessary to ensure that genotypic effects on plant to plant and seed yield variability, and particularly the effects of their distinctive morphological characteristics, could be isolated from agronomic influences.

Thus, the comparison between trials highlights agronomic management as a major source of the yield differences. Whether or not yield differences were associated with variations in the PWT and PHI distributions is examined in Sections 8.2.2 and 8.2.3.

8.2.1.2 Yields comparisons at different populations. Variability in seed and biological yields among crops was also demonstrated by the results of the 1989/90 experiment. It compared the performance of four morphologically distinct pea genotypes sown at five populations, ranging from widely spaced plants (9 plants m^{-2}) to high populations (400 plants m^{-2}), where substantial interplant competition was intended.

There were similar general trends across populations for both seed and biological yields. Significant differences among genotypes only occurred at the two highest populations. Seed yields followed an asymptotic response for genotypes CLU and SLU, rising from about 350 g m^{-2} at 9 plants m^{-2} to 780 g m^{-2} at the highest population (Figure 5.1). The biological yields of these two genotypes were related asymptotically to plant population, increasing sharply from 580 to 1350 g m^{-2} between 9 and 400 plants m^{-2}. From 9 to 100 plants m^{-2}, CVN and SVU produced similar seed and biological yields to the other genotypes. An important result was that at the two highest populations (225 and 400 plants m^{-2}) the yield responses differed among the genotypes under the same agronomic conditions. In particular, at 225 plants m^{-2} SVU produced the lowest seed yield.

At 400 plants m^{-2} genotype CVN produced the lowest seed and biological yields and its seed yield was lower than at 225 plants m^{-2}. Therefore, seed yield for genotype CVN had a parabolic relationship with plant population. The seed yield of genotype SVU was lower than those of CLU and SLU but its biological yield was similar. Interplant competition was the most severe at these two populations, so analysis of individual plant performance and variability in these circumstances is important for determining their consequences for crop yields.

Asymptotic and parabolic relationships between seed and biological yields and plant population have been reported widely for many crops (Holliday, 1960a; 1960b; Donald and Hamblin, 1976) including field peas (Falloon and White, 1978; Cousin *et al.*, 1985). The responses reflect the different capabilities of crops sown at contrasting populations to develop their leaf canopies, and therefore to intercept the radiation required for growth.

8.2.1.3 Summary of yield variability. There were substantial seed and biological yield differences between the crops in the two trials in the 1988/89 and 1989/90 seasons and among population treatments in the 1989/90 experiment. Crop management practices, including the plant population treatments, were the main causes of the differences. However, yield differences were also found among the genotypes under high yield potential conditions with intensive crop management at 225 and 400 plants m^{-2} in the 1989/90 population experiment.

8.2.2 Variability in PWT Distributions Between Crops

To test the initial assumption of this study (Section 1.2), the relationship between the yield differences and variability in PWT and PHI distributions is discussed in the following section. Comparisons of the frequency distributions from these crops are based on estimates of their location (mean and median), dispersion (SD and CV) and deviation from normality (skewness (g_1) and kurtosis (g_2)).

8.2.2.1 Comparisons of PWT values at 100 plants m^{-2}. The differences in biological yields at 100 plants m^{-2} were determined by the PWT values. In the lower yielding 1988/89 trial the mean and median PWT values were between 7 and 10 g (Section 3.2.3) compared with approximately 12.0 g in 1989/90 (Table 5.6). Thus, on average, each plant in the second experiment produced more dry matter and, therefore, had a greater potential seed yield than individuals in the 1988/89 trial. Collectively, these higher PWT values resulted in the higher biological yield in 1989/90.

The shapes of the PWT distributions also indicated differences in seed yields. The normal PWT distributions for genotype SVU in 1988/89 suggested that there was less interplant competition than for genotype CVN, which had a positively skewed distribution (Figure 3.2). It was hypothesized that genotype SVU may possess more characteristics associated with high seed yield than CVN (Chapter 3). This supported the idea that yield variability could be related to differences in the structure of PWT distributions (Ambrose and Hedley, 1984).

When Ambrose and Hedley (1984) proposed a link between seed yield and PWT distributions, their high two yielding genotypes had normal PWT distributions, with median values of 7.4 and 8.1 g. In addition, the PWT distribution of their lower yielding genotype was positively skewed with a median of 5.7 g. The expectation from the results of the 1988/89 trial, and those reported by Ambrose and Hedley (1984) is that crops which have normal PWT distributions produce higher seed yields than those with positively skewed PWT distributions, when grown under similar agronomic conditions.

However, a positively skewed distribution of PWT values can not necessarily be associated with low seed yields. All genotypes in the 1989/90 experiment produced positively skewed PWT distributions, but their seed yields were all about 50 % higher than in 1988/89. These distributions were leptokurtic and had lower CV values (32-40 %) than those from the cultivar evaluation trial (38-58 %). Furthermore, the median PWT

values of these crops were about 50 % higher than those reported by Ambrose and Hedley (1984).

Thus, a combination of both the location and dispersion of the PWT values contributes to the association with seed yield. Similarly shaped PWT distributions which differ in location, and those that differ in shape at the same location are both associated with different seed yields. Further evidence to support this idea was found in the changes in PWT distributions and seed yields at different populations in the 1989/90 experiment.

8.2.2.2 Changes in PWT distributions at different plant populations. The overall effects of increased plant populations on PWT distributions were consistent with previous reports for field peas (Hedley *et al.*, 1983) and for other annual plants (Edmeades and Daynard, 1979; Hawthorn and Cavers, 1982). The degree of positive skewness and CV values increased at higher populations as interplant competition increased.

The location and dispersion of PWT distributions were similar for all genotypes as spaced plants and there were no differences in seed yield (Figure 5.1). The mean PWT was about 66 g for each genotype. However, the results indicate that there was substantial variability in PWT for these field pea crops and this was greater than that observed for other crops. There was a 10-fold range from smallest to largest plants, and competition indices were about 200% (Table 5.7) and CV values ranged from 31 to 46 %. Hedley and Ambrose (1985) considered CV values of this magnitude to be high for field peas. In contrast, for spaced single cross hybrid maize, Edmeades and Daynard (1979) reported CV values as low as 10 % and, for spaced barley plants, Soetono and Donald (1980) reported only a three to five fold range in PWT values. An inherent level of variability for PWT may be a disadvantage for field pea crops and cause low, unstable yields (Hedley and Ambrose, 1984).

The primary effect of increasing plant population from 9 to 100 plants m^{-2} was that seed and biological yields increased. Despite the five-fold reduction in both mean PWT and competition indices (Tables 5.6 and 5.7) the CV values at 100 plants m^{-2} were similar (31-39 %) to those for spaced plants. This indicates that the relative variability of PWT values within the crops was consistent across these populations, and was not accentuated by the increased interplant competition.

Overall, the increased yield potential resulting from the greater leaf area index of the 100 plants m^{-2} population out-weighed any adverse effects of the changes in the location and shape of the PWT distributions.

Further increases in plant population showed that differences in seed yield could be attributed to differences in the location of the positively skewed distributions. The lower seed yield for CVN at 400 plants m^{-2} was associated with a positively skewed PWT distribution (which was similar to that from the other genotypes) but it had lower mean PWT and SWT values (Table 5.6). In contrast, the PWT distribution of SVU was similar in shape and location to the higher yielding genotypes, but the mean SWT was lower.

Effectively, these results support the association of a low seed yield with positively skewed PWT distributions (Ambrose and Hedley, 1984), but also indicate that the location of the PWT and SWT distributions are also important. By definition (Donald, 1963) it follows that an association between PHI and seed yield is also expected. Specifically, populations with large numbers of small plants are expected to produce lower seed yields due to the small plants producing a low PHI (Chapter 3; Ambrose and Hedley, 1984).

8.2.3 Variability in PHI Distributions Between Crops

The assumption of an association between seed yield and frequency distributions for PHI was investigated through comparisons between the results of the 1988/89 and 1989/90 trials, and among populations from the 1989/90 experiment.

8.2.3.1 Comparisons of PHI values at 100 plants m^{-2}. The differences in seed yield among the genotypes in the cultivar evaluation trial, and between the two seasons, were associated with their PHI distributions. Variation in the results between replicates in the 1988/89 trail prevented statistical separation of seed yields by genotype. However, PHI distributions were classified into three distinct categories (Figure 3.1).

Crops that produced a low seed yield were classified in the first category which contained distributions with high numbers of barren and poor performing (PHI $\leq$33 %) plants and had higher CV values than the other categories (Figure 3.1; Table 3.3). In contrast, the second category was bimodal with groups of barren plants and others with PHI values above 33 %. The crops with the highest yield were classified in the third distribution category and characterized by few poor performing plants and relatively low CV values (Figure 3.1). The conclusion from this trial was that both the location and dispersion of PHI distributions were associated with seed yield. Differences in the location and dispersion of SWT, PWT and PHI distributions were therefore all associated with yield differences.

Although the classification of PHI distributions into categories was useful for interpreting results from the 1988/89 trial, none of these categories were observed in the results from the 1989/90 experiment. In 1989/90 all crops planted at 100 plants m^{-2} produced negatively skewed, leptokurtic distributions with a mean PHI of about 60 % and a CV of less than 13 %. Effectively, these were 'ideal' crops with uniformly high PHI values for all plants, and a high seed yield. The differences in the PHI distributions between the two trials again highlights the importance of management in determining the seed yield potential of a crop, and show that it dominates any genotypic differences.

Altogether, four distinct categories of PHI distributions were identified in these two trials. In addition, the high yielding genotypes reported by Ambrose and Hedley (1984) showed a similar structure to those in the third category of the cultivar evaluation trial. In

contrast, their low yielding genotype produced a uniformly flat PHI distribution with nearly 30 % of the plants barren. Ambrose and Hedley (1984) implied that the variability of this low yielding genotype had a genetic basis. Hedley and Ambrose (1984) suggested there was a residual level of variability for PHI within a field pea genotype, even when agronomic causes of variation were minimized. This hypothesis was tested in the 1989/90 population experiment.

8.2.3.2 Effect of plant population on PHI. The spaced plant treatment in the 1989/90 experiment was intended to allow full genetic expression by each genotype and therefore provide a baseline of its innate variability.

The dominant result from the analysis of spaced plants was the uniformly high PHI values for all plants of the four genotypes. The mean and median PHI values were above 56 % with CV values less than 8 %. The characteristics of the spaced plants were analogous to those proposed for the ideal crop, with every plant achieving a high PHI value. A similar result occurred at 49 plants m^{-2}, with PHI values uniformly high but seed and biological yields below the potential for the environment. However, the plants did not produce a closed canopy, so the seed and biological yields were relatively low, even though individual plant performance was maximized. Clearly these results illustrate the balance required between uniformity in the PHI of individual plants and maximising seed and biological yields.

The results at 100 plants m^{-2} were discussed in Section 8.2.3.1. The high yields and uniformity of PHIs illustrate three important points. Firstly, there was no evidence of a genetic predisposition for plant to plant variability in PHI, for any of these genotypes. Secondly, the general responses of seed and biological yields to changes in plant population support previous recommendations of 100 plants m^{-2} as an appropriate sowing population (Stoker, 1975; Jermyn, 1984) for commercial crops. Thirdly, the lack of significant differences in seed and biological yields or PWT and PHI values at 100

plants m^{-2} prevents any discrimination among these genotypes. That is, if 100 plants m^{-2} had been the only population in the trial, as in the cultivar evaluation trial, then none of these characteristics would have had value as a selection criteria for breeders.

At the two highest populations the increased interplant competition did result in different PHI distributions between the genotypes. Most plants still had PHI values close to the physiological maximum of 60-65 %, but there were more plants with low PHI values and consequently a general trend of increased variability in PHI.

The seed yield of genotype CVN declined at the highest population, and had the greatest level of plant to plant variability for PHI. Its CV was approximately double the CVs obtained from the other genotypes. In contrast, the lower seed yield of SVU at higher populations, was due to a lower mean PHI (Table 5.5) rather than increased plant to plant variability; its CV was similar to those of CLU and SLU. Thus, both the dispersion and location of the PHI distributions were associated with a reduced seed yields.

8.2.4 Summary of Variability Within and Between Crops

The original assumption of an association between reduced seed yields and increased variability in PWT and PHI distributions was supported by the trials in this study. Seed and biological yield differences were caused mainly by agronomic factors, but there were also differences in the yield responses of genotypes grown under similar agronomic conditions, particularly at high plant populations.

By examining the frequency distributions of PWT and PHI values, it was shown that yield differences were related to differences in both the location and dispersion of the distributions. However, the nature of these associations was inconsistent among seasons, treatments and genotypes.

Beyond describing differences in PHI distributions, Ambrose and Hedley (1984) offered no guidelines for their classification. Many categories could be defined, so to progress beyond qualitative descriptions, a system capable of quantifying and describing differences in the frequency distributions was required. Therefore, the empirical PAM was proposed to formalize the associations between seed yield and PHI distributions into a testable model that could be used repeatedly to describe field pea crops.

8.3 PRINCIPAL AXIS MODEL

In previous studies (Hedley and Ambrose, 1981; Ambrose and Hedley, 1984) and in the 1988/89 cultivar evaluation trial, a strong linear relationship was found between SWT and PWT. The PAM has been developed based on this relationship with an ellipse calculated to contain a predetermined proportion of the SWT and PWT points. The principal axis of this ellipse was then used to describe the relationship between SWT and PWT.

Through a series of 16 simulations it was shown that changes in the mean and SD of the SWT and PWT distributions representing a crop could be described in terms of changes in the constants used to determine the principal axis and ellipse (Chapter 4). The simulations also highlighted the importance of boundary conditions, based on the biological limits of individual field pea plants (Figure 4.4).

In the following discussion, the implications of differences in the SWT axis intercept, principal axis and ellipse are interpreted in terms of their effects on seed yield. Although the interpretations are based on the components of the PAM, they are considered as consequences of changes in the frequency distributions of SWT and PWT values produced from a crop. One objective is to determine if the differences in seed yield between crops in this study could be described in terms of the components of the PAM. A second objective is to identify changes in the components that would be associated with improved seed yield.

The position of the SWT axis intercept is discussed because it is central to the hypothesis of a MPW for field peas (Section 8.3.1). Following this, differences in the seed yield of crops are related to components of the PAM (Section 8.3.2). The significantly lower seed yields found for genotypes SVU and CVN in the 1989/90 population experiment (Figure 5.1) are explained by differences in the components of the PAM. In addition, differences in seed yield resulting from water stress, and changes in plant populations, are also interpreted in terms of differences in the components of the PAM.

The discussion leads to the separation of a general crop stress from a specific plant stress within a crop. The idea of separate general and specific stresses is illustrated further by using the PAM to describe the effects of virus infection on the seed yield of individual plants and the crop (Section 8.3.2.5).

8.3.1 Location of the SWT Axis Intercept and Existence of a MPW

The simulations showed that the position of the SWT axis intercept influenced the relationship between PWT and PHI values. If the intercept is negative then the value of the slope of the principal axis also represents the upper asymptote for the relationship between PHI and PWT and a MPW is calculated. For small plants, the MPW represents a greater proportion of their PWT and consequently their PHI is lower. If the SWT axis intercept is zero then no MPW is calculated, and PHI values are independent of PWT. If the SWT axis intercept is positive then the slope represents a lower asymptote (Section 4.5).

The position of the SWT axis intercept is a contentious issue. Gardner and Gardner (1983) considered the intercept was probably species dependent, but generally negative, and influenced by environmental factors. Consequently, they proposed that a MPW does exist, and, therefore, PHI values are dependent on PWT. This view was opposed by Prihar and Stewart (1991) who considered negative intercepts only resulted because

stressed plants had been included in analyses of the relationship between SWT and PWT. They concluded that a MPW was not species dependent. An important aim of the 1989/90 plant population experiment was, therefore, to determine whether the intercept for field peas was negative, positive or zero and consequently determine the effect on PHI values.

The widely spaced plants in this trial were included to represent plants in an environment free of stresses from agronomic factors and interplant competition. The conclusions of Prihar and Stewart (1991) meant that the SWT axis intercepts from this treatment should be zero or even positive. In fact the opposite result occurred. The largest negative intercepts and MPW values were calculated from this treatment. The negative values may have resulted from intraplant competition whereby branches competed for resources in a similar manner to individual plants at higher populations (Section 6.4.6).

The results from spaced plants illustrate two problems that are likely to be encountered whenever the position of the SWT axis intercept, and the existence of a MPW, is investigated. Firstly, it may be impossible to examine multi-stemmed or tillered plants in an environment completely free from some form of stress because of intraplant competition from the vegetative structures. Secondly, where interplant competition is not present, the spaced plants represent points located away from the PWT axis intercept. Thus, considerable extrapolation is necessary to infer the MPW. For example, mean PWT values were approximately 60 g plant^{-1} at 9 plants m^{-2}, but the MPW values were estimated to be 1 to 3 g plant^{-1}. To examine the region from which the MPW is calculated, plants of low PWT are required. However, to produce these small plants some form of external stress is necessary, such as high plant populations. Consequently determination of a species dependent MPW will be confounded by stress from interplant competition.

To investigate the existence of a MPW for field peas, a compromise population of 100 plants m^{-2} was used. At this population, 80 % of the plants were single stemmed with the

remainder having one branch (Table 6.1). Interplant competition was implicated by the decreases in the competition indices and mean PWT values from those found at 9 plants m^{-2}, and by the increase in positive skewness of the PWT distribution (Table 6.4). However, the consistency of PHI values between 9 and 100 plants m^{-2} indicates that the effects of competition were similar for each plant at 100 plants m^{-2}.

This treatment represents a recommended commercial population and was, therefore, analogous to the sorghum crops Prihar and Stewart (1991) considered non-stressed and which did not produce negative intercepts. In contrast to that result, all SWT axis intercepts were negative at this population. Indeed, under well managed, non-water stressed conditions, 19 of the 20 treatments in this experiment resulted in negative SWT axis intercepts, which supports the existence of a MPW for field peas. These results for field peas also support the views of Gardner and Gardner (1983) that MPW values are higher for large seeded species.

Further support for the association of MPWs with large seeded species can be derived from results for *Plantago ovata*. This species has a 1000 sw of about 1.6 g compared to 200 g for field peas. No MPW was detected for *Plantago* and mean PHI values were found to be about 20 % for both the lightest (PWT=0.8 g) and heaviest (PWT=20 g) groups of plants (McNeil *et al.*, 1993; in press).

In terms of the PAM, the SWT axis intercept for *Plantago* would be at the origin with PHI values independent of PWT. The inconsistent results for sorghum, with both positive and negative SWT intercepts (Gardner and Gardner, 1983; Prihar and Stewart, 1991), supports the idea that the MPW is affected by environmental factors. For field peas, the MPW values from the water stressed cultivar evaluation trial were about 1.5 g higher, or approximately double those from the equivalent treatment in 1989/90.

By focusing on the validity of calculating MPW values, Prihar and Stewart (1991) have shifted attention from the effects of the MPW on yield. Regardless of whether the MPW

is species dependent or occurs due to stress within crops, the influence on PHI values is the same. A negative SWT intercept results in an asymptotic relationship between PHI and PWT (Gardner and Gardner, 1983; Prihar and Stewart, 1991). The slope of the regression line between SWT and PWT then provides an estimate of the maximum mean PHI, and therefore CHI, of a crop. In terms of the PAM, the location of PWT values, represented by the ellipse, is then the dominant factor in determining the effect of the MPW on the individual PHI values, and consequently the CHI and seed yield of the crop. Greater variability is expected when the PWT is low and when the ellipse is modified by the PWT axis boundary.

8.3.1.1 Summary of SWT intercept data.

Two problems were encountered when investigating the hypothesis of a MPW for field peas. Firstly, when plants were grown in an environment free of stress from interplant competition, intraplant competition occurred. Secondly, considerable extrapolation was necessary to estimate the value of the PWT axis intercept. To reduce the extent of extrapolation, increased plant populations were used. The resulting PWT values were located closer to the PWT axis intercept, but with increased interplant competition also apparent.

Despite these problems, a negative SWT axis intercept was consistently detected from the field pea crops grown for this study. This result supports the existence of a MPW for field peas, and for large seeded crops generally. A direct consequence of detecting a MPW is that individual PHI values within a crop are then affected by their PWT (Section 4.5).

8.3.2 PAM to Describe Differences in Seed Yield

A strong linear relationship between SWT and PWT has been found for many crops (Section 2.4.2). However, because a negative SWT axis intercept was found for field peas, the intercept and slope must both be considered when comparing crop performance.

The slope provides an estimate of the maximum mean PHI, and therefore CHI, of a crop. In this section the lower seed yield produced by genotypes SVU and CVN (Chapter 5) are explained by differences in the components of the PAM.

8.3.2.1 Genotype SVU. The lower seed yield of genotype SVU is explained by the lower slope of its principal axis relative to the other three genotypes (Table 6.2), particularly at 400 plants m^{-2}. This genotype produced a similar biological yield and mean PWT to the higher yielding genotypes but converted a lower proportion of this dry matter to seed. As a consequence, the individual PHI values for each plant were lower than in the higher yielding genotypes, but the CV was similar (Table 6.5). This supports the previous association of the lower seed yield with a shift in location of the PHI distribution (Section 8.2.3.2), and not an increase in the variability of PHI. In terms of the relationship between PHI and PWT, the lower seed yield for SVU was reflected in a lower asymptote.

8.3.2.2 Genotype CVN. The slope of the axis for genotype CVN was similar to the high yielding genotypes (Table 6.2), and does not explain its lower seed yield at 400 plants m^{-2}. However, the lower yield can be explained by a combination of the lowest mean PWT and highest MPW. The low mean PWT indicates that the ellipse representing these plants was located closer to the PWT axis boundary than in the other genotypes. The consequent effect on PHI values can be interpreted from the asymptotic relationship between PHI and PWT.

The PHI was close to the maximum for most of the plants, and near the asymptote. However, the small plants for CVN were located further down the initial linear phase of this relationship than in other genotypes. The influence of the MPW was, therefore, greater (Section 4.5), and small differences in the PWT resulted in large differences in PHI. The effect on PHI was shown by the mean value, which was 8 % lower than from the two high yielding genotypes, and by the CV, which was double those of the other

three genotypes (Table 6.5). Thus, the lower seed yield of CVN resulted from a squeeze between the lowest mean PWT and highest MPW. In terms of the PAM, the ellipse was located closer to the PWT axis boundary than for the other genotypes.

8.3.2.3 Water stress. The effects of water stress on crops can also be described using the PAM. The non-water stressed crops grown in 1989/90 had a higher seed yield, lower MPW values and higher slopes than the water stressed crops in 1988/89. By definition, the lower slope in 1988/89 also indicates a lower asymptote for the relationship between PHI and PWT. Thus, for the same PWT value the SWT and, therefore, PHI was lower for plants grown in 1988/89.

It follows that increases in the severity of water stress would probably be expressed as increases in the MPW, and decreases in the slope of the axis. An irrigation experiment with controlled levels of water stress may result in a series of principal axes with the slopes declining and the MPW increasing as the severity of water stress increases.

The location and size of the ellipse must also be considered when describing the effects of water stress. In 1988/89 the mean PWT and R^2 were lower than in 1989/90 (Tables 3.4 and 6.2). Thus, an ellipse with a larger axis ratio and located closer to the origin results from this stress. The changes in the ellipse reflect two important biological differences within the crops. Firstly, the lower mean PWT in 1989/90 indicates a greater influence of the MPW on PHI values, and consequently seed yield (Section 4.5). Secondly, the increased deviation around the principal axis indicates that the effect of water stress varied between plants.

Thus, the impact of water stress may be described by changes in both the principal axis and ellipse. The axis represents the average effect of stress on the seed yield of all plants in the crop, and the deviations around the axes (represented by the ellipse), then indicate a specific stress on individual plants within each crop. For SWT values located above

the principal axis the affect of water stress was less than average. Conversely, for SWT values below the principal axis the stress was greater than average.

Discussions of the impact of stress on a crop should therefore consider both the general stress affecting all plants and the specific stress experienced by individual plants.

By definition, different SWT values at the same PWT will result in different PHI values. Thus, increased specific stress would also be expressed as an increase in PHI variability. The separation of general and specific stress can be further illustrated when the PAM of used to interpret the effects of changes in plant population, and viral infection of individual plants on the crops.

8.3.2.4 Changes in plant population. The increases in plant population from 9 to 400 plants m^{-2} increased the stress from interplant competition on all plants. The extent of competition was shown by the 20-fold reduction in mean SWT and PWT values, and the decreases in competition indices from 200 to 12 % (Table 5.6 and 5.7).

The increased interplant competition was also reflected as an increase in the general stress on plants, but virtually no change in the specific stress. That is, the ellipse shifted towards the PWT axis intercept but the decreases in the projected lengths on both axes were similar (Figure 6.2). Furthermore, only small changes in the slope of the principal axis were observed (Table 6.2), and consequently, the SWT and PHI values predicted for any PWT value were similar at all populations.

The high R^2 values at all populations was the dominant result from the analyses of changes in plant populations. This implies that interplant competition affected all plants equally within each crop. Non-uniform planting patterns may cause a higher degree of specific stress than was observed in this study.

8.3.2.5 Virus infection. The PAM can also be used to interpret the effects of virus infection on individual plants, as a further example of specific stress. The extent of stress for individual plants can be quantified by a comparison of the SWT from infected plants to that predicted from the regression analyses of the virus free plants. The infected plants had SWT and PHI values below those predicted from the initial regressions (Chapter 7).

A limitation of this description of specific stress is that it only relates to reductions in reproductive growth. The location of most infected plants near the PWT axis intercept indicates that vegetative performance was also reduced by the viral infection. In addition, simply including infected plants in the regression analysis of SWT against PWT may cause leverage (Chapter 7).

8.3.2.6 Summary. The original aim of developing the PAM was to formalize the relationship between PHI distributions and seed yield. The PHI values were separated into SWT and PWT distributions and incorporated into the PAM. The objective was then to determine whether differences in seed yield could be described by differences in the components of the PAM.

Separate components of the PAM were used to describe the seed yield differences between genotypes in the population experiment. The lower seed yield of genotype SVU was reflected in the lower slope of the principal axis. In contrast, the lower yield from CVN was explained by a combination of a lower mean PWT and higher MPW. Thus, the ellipse position reflected the lower seed yield.

The PAM was also used to describe the effects of changes in plant population, water stress and virus infection on crops. The axis position was consistent for each genotype across all populations tested, and changes in the ellipse location were identified as the important component for explaining the effects of increased populations. However, the dominant result was the lack of deviation from the axis at all populations.

The effects of water stress were described by a decrease in the slope, higher MPW and greater variability in points around the principal axis. It was subsequently proposed that the total stress experienced by a plant should be separated into general and specific stresses.

The position of the axis and ellipse indicates the overall effect of a general stress on all plants within a crop. The specific stress is then defined as the stochastically determined stress experienced by individual plants, indicated by the deviation in their position from that predicted from the principal axis. The implication is that plants with a SWT value below the axis have experienced a greater specific stress than average.

The differences in components of the PAM can also be related back to their impact on the PHI distributions for each crop and subsequently used to identify mechanisms for yield improvement. The lower slope of the principal axis for SVU resulted from the increase in general stress from interplant competition, with no apparent increase in the specific stress. This result is consistent with the lower mean PHI but similar CV found for its PHI distribution (Section 8.2.3.2).

In contrast, increased general stress combined with minimal specific stress resulted in greater variability in the PHI values for genotype CVN. This was due to the shift in location of the ellipse and the subsequent increase in the influence of its MPW value.

Greater variability in PHI values was also reported from increased specific stress, illustrated by the effects of water stress and virus infection. Thus, the PAM was used to identify the effects of two separate influences that caused variability in the PHI distributions.

It follows that decreasing this variability in PHI and improving seed yield would result from:

1) decreasing the MPW (increase in SWT axis intercept),
2) increasing the slope of the principal axis,
3) minimizing the deviation around the principal axis,
4) optimizing the ellipse location.

8.4 PAM FOR IMPROVING YIELD

The PAM has been developed and used as a statistical tool to describe the performance of individual plants within a crop. From these descriptions, four criteria were identified that could be used to improve seed yields. The remainder of this discussion examines the final objective of this study, which is to identify possible selection criteria for use in a breeding programme. The initial section (8.4.1) outlines previous attempts to identify selection criteria that were based on the relationship between SWT and PWT. Section 8.4.2 gives a method for selecting between field pea genotypes, based on the PAM. Finally, differences in the components of the PAM are related to morphological and physiological differences observed among the genotypes in this study (Section 8.4.3).

8.4.1 PAM and Plant Breeders Objectives

Support for using the components of the PAM as a basis for selection to improve yield can be inferred from previous proposals based on the relationship between SWT and PWT. Gardner and Gardner (1983) indicated that plant breeders have developed increased drought adaptation and improved yield through decreasing the SWT axis intercept and increasing the slope of the axis. However, in most cases, these changes described the results of breeding and were not necessarily the aims.

The goal of high but stable PHI values for field pea plants (Ambrose and Hedley, 1984) will result from minimising the deviation around the principal axis and optimizing the position of the ellipse. Ambrose and Hedley (1984) were mainly concerned with interplant competition increasing the specific stress in a crop, as indicated by variation around the axis. However, in this study the investigations using the PAM indicated that high PHI variability may also occur through a general stress on all plants in a population, as shown for genotype CVN. Thus, the location of the ellipse must also be optimized to improve seed yields.

It follows that the breeding objective of producing improved high yielding cultivars, by selecting plant types that produce these high, stable PHI values for all plants within a crop, can be targeted in terms of the PAM. The 'ideal' crop would be represented by a principal axis with a slope equal to the physiological maximum PHI for a genotype. In addition, the SWT axis intercept would be at the origin and there would be no deviation about the principal axis. The location of the ellipse would optimize the biological yield for a given environment and consequently the seed yield would also be maximized. Which of these factors is most important for achieving the maximum seed yield will vary depending on the genotype and the environment.

For example, McNeil *et al.* (1988) considered the possibility of a reduction in PHI variability as the basis for yield improvement in the largely unimproved species *Plantago ovata.* For this species, a wide range of PHI values (0-35 %), centred around a mean value of about 20 %, was found for plants ranging from 0.1 to 30 g (McNeil, 1991). Thus, although their crop management had aimed to maximize yield, a high range of PHI values was found. In terms of the PAM, this crop would be represented by a principal axis starting at the origin, increasing with a slope of 0.2, but with a high degree of scatter about the line.

Describing this crop in terms of the PAM highlights two mechanisms for improving seed yield. Either a reduction in the scatter about the axis or an increase in its slope would

increase the mean PHI. Because the SWT axis intercept was at the origin, the ellipse location was not important and PHI was independent of PWT. The maximum PHI values found for *Plantago*, indicated that the potential exists for a slope of at least 0.35. Continued selection and domestication of this species is likely to result in further increases in the mean PHI.

8.4.1.1 Crop selection based on PAM. Prihar and Stewart (1990) suggested that plant breeders should calculate a genetic harvest index (GHI) to discriminate between cultivars, based on the slope of the SWT versus PWT relationship. This GHI was calculated as the slope of a line from the origin to the maximum CHI for each cultivar, with the assumption that the SWT axis intercept is zero. Prihar and Stewart (1991) contended that a negative SWT axis intercept is an artefact of including plants that experienced different levels of stress in previous calculations of the relationship between SWT and PWT.

This assumption was not supported by the results for field peas, where a MPW was consistently evident, even when minimal specific stress was detected (Section 8.3.1). Furthermore, if Prihar and Stewart (1990) had used individual plant data rather than data from whole crops, analyses for at least some of the crops may have resulted in negative SWT axis intercepts. By only presenting CHI values, any association between PHI and PWT values was hidden.

Where a negative intercept exists selection must be based on a combination of both the intercept and slope, with the axes ratio and ellipse also considered (Section 8.3.2.6).

Genotype selection based on evaluation of seed yield usually begins in the F5 or F6 generations for field peas, when crops are screened at commercial plant populations. Genotypes with the highest seed yields are selected. This method produces no information on the performance of individual plants within the crops. A high seed yield

may result from anywhere between the situations of a few dominant plants producing the majority of seed or a similar performance from all plants in the crop.

Ambrose and Hedley (1985) suggested that the structure of the population is important, and that it must be assessed if seed yield instability between seasons is to be reduced. They highlighted interplant competition as a possible contributor to yield instability. Their argument was that this competition would be amplified in unfavourable seasons or under poor agronomic conditions, and therefore contribute to low yields.

Selections based on consideration of the components of the PAM, rather than solely on seed yield, may contribute to the selection of genotypes which are more tolerant of stressful conditions, and consequently produce more stable yields. Growing crops at high populations in yield trials may assist the identification of tolerant genotypes. In this study, genotypes CLU and SLU only expressed their superior seed yields and, greater tolerance to interplant competition at 400 plants m^{-2}.

To this point the GHI and PAM have been used to indicate possible approaches for selecting genotypes on the basis of crop performance. In fact, the definition of a GHI seems inappropriate given that it is only defined at the crop level. To assist selections between genotypes at the individual plant level, an alternative method based on the PAM is proposed.

8.4.2 Plant Selections Based on PAM

In the early generations of a field pea breeding programme (F2-F4), selection for yield potential is a low priority. Most attention is focused on the elimination of agronomic defects and susceptibility to diseases. Yield assessment assumes higher priority in the F5 and F6 generations (Jermyn, 1987) when sufficient material is available for comparisons between genotypes in plot trials. The genotypes in these trials are from

earlier selections of superior performing single plants which are usually competitive, dominant types (Ambrose and Hedley, 1984; Wilson, 1987).

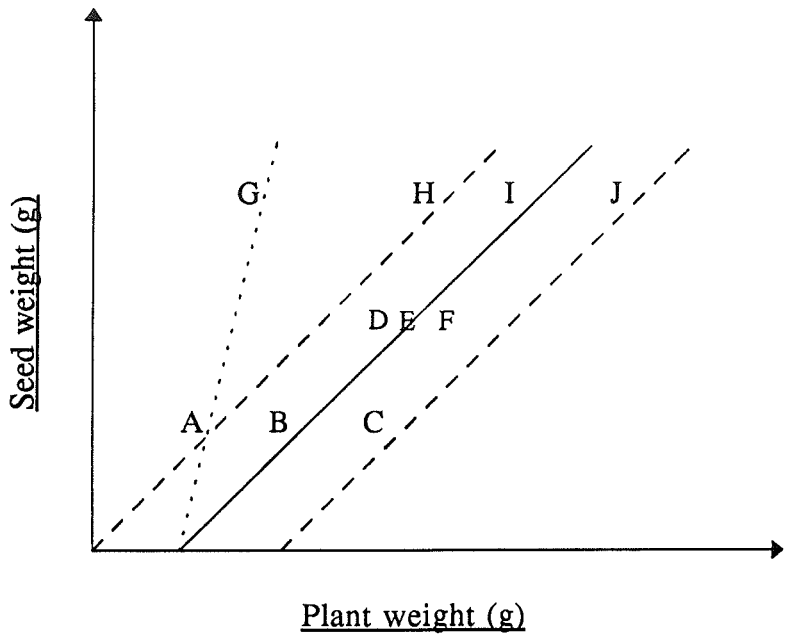
However, it is hypothesized plants which are weak competitors, may be preferred plant types for use in crops (Donald and Hamblin, 1976, 1983; Ambrose and Hedley, 1985; Wilson, 1987). However, these plants are usually eliminated before yield trials due to their poor performance as individuals. The proposed method of selection using the PAM is therefore based on individual plant performance, but not necessarily plant size.

8.4.2.1 Example of plant selection based on PAM. The initial step is to grow individual plants and measure their SWT and PWT at harvest. The analysis and selection is independent of the population at which plants are sown. However, the inconsistency of yield component results, and reductions in branching, SWT, PWT and CHI values observed in this study, suggest that a commercial population should be used. In addition, the generation at which selection occurs does not affect the analyses using the PAM, but the influence of heterozygosity in field peas indicates that the F4 generation may be appropriate, after major defect elimination has occurred, but without exclusion of weak competitors.

The SWT and PWT data from all plants are included in the analyses using the PAM. Selection is then based on the position of each plant relative to the average for the population, which is represented by the principal axis.

The process of selection is illustrated using points of reference from Figure 8.1. In this example the principal axis is depicted with a negative SWT axis intercept. The points A-J represent the locations of hypothetical genotypes that could be selected. The performance of each individual plant is determined by its slope and intercept, relative to the rest of the population. The preferred plants for selection will be those with the highest slope and lowest intercept.

Figure 8.1: PAM for selecting between individual plants in a breeding programme. Letters A-J represent the relative positions of individual genotypes.



A line is drawn from the PWT axis intercept to each point. The highest ranking plants have the highest slopes (Table 8.1). On this basis, points A and G are considered to have equal merit, as are points D and H, even though in each case their absolute SWT and PWT values are very different. Points B, E and I represent the average of all plants, because they are on the principal axis. Points C, F and J are all below the average line, so receive the lowest ranking.

The intercept position is estimated relative to the principal axis. A line with the same slope as the principal axis is drawn from each point to the PWT axis intercept. Those with the lowest PWT axis intercepts receive the highest rankings (Table 8.1). Equally, the rankings can be attained from the residuals of the points. Those with deviations above the line have positive residuals. Points are ranked from those with the largest positive residual to those with the largest negative residual. The deviation from the principal axis is measured either parallel to the SWT axis or at a 90° angle, depending on the regression method (Sokal and Rohlf, 1981). The combined total of these rankings is

used for selection. In this example, plants represented by points G, A, H and D would be selected in that order ahead of the rest (Table 8.1).

Table 8.1: Ranking of individual plant performance in a breeding programme based on the components of the PAM and the GHI compared to SWT (Figure 8.1).

Point	Method of Ranking					
	Slope (S)	Intercept (I)	S + I	PAM	GHI	SWT
A	1	2	3	2	2	8
B	5	5	10	5	9	8
C	10	9	19	10	10	8
D	3	4	7	4	4	5
E	5	5	10	5	6	5
F	8	8	16	8	8	5
G	1	1	2	1	1	1
H	3	2	5	3	2	1
I	5	5	10	5	5	1
J	8	9	17	9	7	1

These selections differ in several ways from those that could be expected from conventional, qualitative selection techniques. Point G is likely to be an obvious selection using any criteria, but discriminating between the remaining points is less obvious. Selecting either large, vigorous plants or those with high harvest indices or high SWT would rank points H, I and J ahead of A, B and C, which have low PWTs and are likely to have PHI values influenced by the MPW. The major difference between selection based on qualitative assessment and that based on the PAM is the ranking of points A and J.

Although point J represents a larger plant, with a higher PHI then point A, the SWT is actually lower than expected from its PWT. In contrast, point A has a lower PWT and PHI than point J, but its SWT is high relative to plants of similar dry weight in the population. Point A represents a weak competitor with poor performance. However, this plant may be more suitable in a crop situation (Donald and Hamblin, 1976; Hedley and Ambrose, 1985) than larger plants. The screening of genotypes based on the PAM therefore gives a quantitative approach for selecting small plants that would usually be excluded from yield trials.

An assumption of this method of selection is that the deviations are genetically based and do not simply reflect the specific stress within the trial. A further assumption is that the position of each point has resulted from a difference either in their slope or intercept. Equally feasible is that the coordinate is the result of a combination of both factors. Separating the contribution of each factor can be achieved by comparisons of crops in later generations.

In this example, the slope and intercept have been assumed to be equally important in determining seed yield. Final rankings were therefore simply the sum of the individual rankings. If one factor is found to be more important than the other, the rankings could be weighted accordingly. An example of this is when the SWT axis intercept is zero, so only the slope is important. The method of analysis is then analogous to the GHI method (Prihar and Stewart, 1991), but uses individual plants (Table 8.1). In this situation point G would still rank first, but A and H would rank equally (Table 8.1). Therefore, with only the slope considered, a group of points that would previously have ranked below point A for slope, but above it for intercept, would now all rank ahead of it (Figure 8.1). Thus, the position of the SWT axis intercept is an important factor in selections based on the PAM.

Overall the PAM has been used to compare genotypes as individual plants and as crops. The PAM is a statistical tool for synthesising information. The practical implications of this method can only be assessed once it has been fully field tested.

The final challenge of this study is to determine whether specific characteristics of the genotypes CVN, CLU, SVU and SLU can be classified as either detrimental or beneficial to the selection of genotypes. The aim is to determine whether the differences in the components of the PAM found in the comparisons of genotypes in the plant population experiment, can be attributed to specific plant types or morphological characteristics.

8.5 SELECTION CRITERIA

8.5.1 Yield Components

The selection of field pea genotypes for improved yield has generally focused on yield components. Analyses of yield components in this study highlighted two important points. Firstly, the yield components exhibited great plasticity and there were large genotype by environment interactions. Secondly, the performance of genotypes with respect to yield components as spaced plants bore little resemblance to their performance at commercial or high populations. Thus, yield components did not prove to be suitable criteria for differentiating between these genotypes.

8.5.2 Field Pea Ideotype

The remainder of this discussion focuses on other biological characteristics of the genotypes from the 1989/90 plant population experiment. The analyses of crop growth and plant growth (Chapter 7) highlighted several characteristics that may have contributed to the yield differences among these genotypes at the two highest populations. The objective is to define characteristics that may be included in a field pea ideotype.

8.5.2.1 Leaf type. The results from this study indicate that conventional and semi-leafless genotypes were equally useful plant types. Low unstable yields for field

peas have often been associated with conventionally leafed plant types (Section 2.1) that are more susceptible to lodging. However, yield reductions through lodging did not occur in any of the genotypes in this study.

The introduction of semi-leafless genotypes was expected to improve standing ability and lead to yield increases (Cousin *et al.*, 1985) through less interplant competition than in conventional leaf types (Section 2.3.2). However, results at 400 plants m^{-2} showed that both the highest and lowest yields were produced from the conventionally leafed plant types, and also that significant yield differences were found between the two semi-leafless genotypes.

Furthermore, the lack of differences in yields among the genotypes at 9 and 49 plants m^{-2} implies that PAR interception was similar for both, even though full canopy closure was not attained. This supports the previous finding of similarities in growth rates between genotypes with these two leaf types (Pyke and Hedley, 1983; 1985; Snoad, 1981).

8.5.2.2 Seedling vigour. The low yielding genotypes in this study were both also classified as having vigorous seedling growth at all populations. This seedling vigour was characterised by earlier emergence, greater ground cover by each plant within the crop, and heavier, taller plants at 32 DAS. However, this seedling vigour did not translate into greater seed or biological yields even though earlier canopy closure was expected.

The implication from these results is that seedling vigour was detrimental to seed yield. A comparison of the growth and development of genotypes CVN and CLU highlighted the major difference as this seedling vigour. For CVN, this greater vigour probably resulted in the lower competition index, lower mean PWT and consequently the greater PHI variability and lower seed yield observed at 400 plants m^{-2}.

Seedling vigour may therefore be an early indicator of the expected interplant competition within a crop. Selection of weak competitors as a basis for an ideotype (Donald, 1968; Sedgley, 1991) could therefore be based on comparisons of their emergence rates and the subsequent development of ground cover from seedlings. It follows that the suggestion that crop management of field peas should aim to maximize the duration of growth through earlier canopy closure (Wilson, 1987), should be interpreted to mean through adequate planting populations of low vigour plants and not through increased seedling vigour.

8.5.2.3 Duration of crop growth. The duration of crop growth was 7 days shorter than for SVU than for SLU, but their reproductive phases were the same length. However, the onset of flowering for SVU may have occurred before canopy closure. The total PAR intercepted during the reproductive phase may, therefore, have been lower than for SLU. Despite the shorter duration of growth, the biological yield of SVU was similar to SLU at 400 plants m^{-2}, although its seed yield was lower.

Thus, early flowering of a genotype, to allow partitioning to seed when interplant competition is low (Ambrose and Hedley, 1984) would be a positive attribute for a field pea ideotype provided it does not result in a decreased total duration of crop growth.

8.5.2.4 Vegetative structures. The suggestions that a field pea ideotype should be non-branched, or late branching (Ambrose and Hedley, 1984; Snoad, 1985) and moderately short (Cousin *et al.*, 1985) were supported by results from this study. The indications from analyses of spaced plants was that there was an energy cost to the plant associated with the production of branches, and that intraplant competition occurred between these branches (Section 6.4.6). Increasing plant population to 100 plants m^{-2} suppressed branching without reducing yields. Siddique and Sedgley (1985) found a similar result for Chickpea, with harvest index and seed yield increasing as branches were eliminated at higher populations.

8.5.3 Summary of Selection Criteria

Analyses of the yield components of field pea crops highlighted their plasticity and inability to be used as a basis for differentiating among these genotypes. In contrast, the characteristics identified as suitable for a field pea ideotype in this study were consistent with those previously proposed (Ambrose and Hedley, 1984; Snoad, 1985; Cousin *et al.*, 1985). An ideotype should be a weak competitor as a single plant, with either a conventional of semi-leafless leaf type, and non-branched or late branching.

In this study the genotypes with low seedling vigour, suffered less from competition and had higher seed yields at 400 plants m^{-2} than the vigorous genotypes. Thus, low seedling vigour may be a positive attribute for a field pea ideotype. In addition, results from the analyses of the duration of crop growth indicated that early flowering would be a favourable characteristic provided it did not also induce earlier maturity.

8.6 CONCLUSIONS

1) Differences in seed yield were explained by differences in the location and dispersion of PWT, SWT, and PHI frequency distributions. However, these associations were less defined than those previously reported (Ambrose and Hedley, 1984).

2) There was a strong linear relationship between SWT and PWT values within each crop analyzed in this study. Indeed, the lack of variation in this relationship was the dominant result from the 1989/90 population experiment.

3) This linear relationship was utilized in the development of the empirical (PAM). The PAM was used to describe systematic changes in the mean and standard deviation of SWT and PWT distributions in terms of their effect on the principal axis and ellipse of the model.

4) The principal axis of the model consistently had a negative SWT axis intercept for field pea crops. This indicates that a MPW exists and, therefore, that the relationship between PHI and PWT was asymptotic. The PHI of an individual plant is therefore dependent on its PWT.

5) Variability in seed yield, due to both agronomic and genotypic factors, could be described in terms of differences in the components of the PAM. In particular, the lower yield in th. 8/89 trial was reflected in higher MPW values, a lower slope of the principal axis.

6) The lower seed yield of genotype CVN was described by a negative shift in the location of the ellipse (as indicated by a significantly lower mean PWT) and a higher MPW. Together these factors explained the lower biological yield and higher PHI variability that was also observed for genotype CVN. In contrast, the lower seed yield for genotype SVU was explained by a lower slope in the principal axis, which reflected the consistently lower PHI values for all plants in the crop.

7) Two separate mechanisms for explaining PHI variability within crops were observed. First, plants of the same PWT had different SWTs. This was expressed as variation around the principal axis and was associated with specific stress, whereby individual plants experienced differing levels of stress during their reproductive growth. Second, small plants produced lower PHI values than large plants due to the influence of the MPW. Thus, PHI variability can occur even when a strong linear relationship exists between SWT and PWT.

8) The PAM could be used to give a quantifiable basis to the selection of genotypes in a field pea breeding programme. In particular, the method is independent of PWT and does not automatically exclude plants that have low PWT and PHI values.

9) The components of yield for field peas could be used to describe crops, in this study but there was no association in this study between seed yield differences and individual components. Screening of these field pea crops could not be based on differences in yield components.

10) The characteristics previously proposed for a field pea ideotype were supported by this study. Ideal plants should be weak competitors with early flowering and should have long growth duration. However, excessive seedling vigour may be a negative characteristic which leads to interplant competition and consequently reduced yields.

11) Interplant competition within crops accentuates delays in emergence, with later emergence generally associated with lower PWT and lower PHIs.

12) Of the four genotypes tested in both the 1988/89 and 1989/90 experiments, the two low vigour genotypes (CLU and SLU) had greater potential than the vigorous genotypes for achieving high, stable yields for all plants when grown at commercial or higher plant population.

8.7 RECOMMENDATIONS FOR FUTURE RESEARCH

1) The general applicability of the PAM concept needs to be examined by conducting similar tests with different crops in different environments.

2) The degree of uniformity between plants in the 1989/90 experiment was greater than expected. There is a requirement to study the agronomic factors that contribute to the degree of plant to plant variability in crops, and to develop recommendations to minimise it. In particular, the role of uniformity in seed placement in plant populations requires further investigation.

3) This high uniformity eliminated any possibility of interaction between plant types and variability in the arrangement within a plant stand. A future experiment should investigate the interaction of plant type with inequalities in the plant arrangement at sowing.

4) The proposed screening method based on the PAM should be evaluated in a breeding programme, firstly by using the slope from the intercept to individual points as a selection criterion and, secondly, by selecting genotypes based on their morphological characteristics.

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Appendix I: Comparison data for PHI and principal axis values used in the development of the principal axis model in Chapter 4. Mean PHI values were calculated from Equation 4.9. *Difference values represent the difference between mean PHI values calculated from Equations 4.09 and 4.10. Principal axis values were calculated from least squares regression methods. †Values represent the difference between the coefficients from principal axis and least squares regression methods (Section 4.6).

Simulation	PHI (%)		Principal axis values			
	Mean	*Difference	Intercept		Gradient	
A	54.3	0.2	-0.43	0.34†	0.59	0.03†
B	18.0	0.1	-12.23	-0.97	0.59	0.03
C	174.3	0.7	11.61	-0.48	0.59	0.03
D	58.0	0.2	-0.20	1.00	0.59	0.03
E	53.7	0	-0.60	-0.33	0.60	0.03
F	17.7	0	-12.61	-0.99	0.60	0.03
G	173.6	5.3	11.40	-0.34	0.60	0.03
H	57.6	0.4	-0.60	-1.02	0.60	0.03
I	54.7	-0.1	-6.60	-1.53	1.21	0.15
J	18.0	0.3	-30.8	-4.60	1.21	0.15
K	174.7	0.4	5.40	-1.53	1.21	0.15
L	58.0	0.3	-18.8	-4.6	1.21	0.15
M	55.9	0.7	2.64	-0.05	0.29	0.01
N	18.8	-0.3	-3.22	-0.15	0.29	0.01
O	175.9	6.3	14.64	-0.05	0.29	0.01
P	58.8	0	8.78	-0.15	0.29	0.01
Q	19.1	-9.2	-0.53	-0.05	0.59	0.03
R	23.9	-4.3	-0.28	0.04	0.46	0.02
S	52.9	0.6	-0.26	-4.45	0.56	0.44
T	51.4	0.3	-1.42	-6.64	0.66	0.66

Appendix II: Soil test results from the 1989/90 plant population experiment. Units vary for each element but are all in g/y ml extract. Summary ranges for interpreting these results are given. The pH was 5.3.

Nutrient	Units	Result	Summary ranges		
			Low	Medium	High
Ca	$y = 1X10^6$	6	6-12	13-25	26-50
P	$y = 4X10^4$	9	9-15	16-25	>26
K	$y = 2.5X10^5$	8	4-5	6-8	9-12
Mg	$y = 2X10^7$	20	0-3	4-10	>11